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POPULATION STRUCTURE, SOCIAL BEHAVIOR, AND ENVIRONMENTAL RELATIONS IN A NATURAL POPULATION OF THE BEACH MOUSE (*PEROMYSCUS POLIONOTUS LEUCOCEPHALUS*)

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INTRODUCTION

THE social structure of species populations has important effects on the potential dissemination of new (mutant) characters. Local differentiation within the species population may be influenced in some part by social behavior. Such phenomena as territoriality, home-range size, population densities and resultant population pressures, fixity of home range, and dispersal tendencies of maturing young all may have a bearing on the rate of spread of mutant characters through a species population. Few of these phenomena can be studied in the laboratory. Field studies are necessary, in spite of the various complexities, the lack of critical control over the experimental animals, and the other inherent difficulties.

Measurements and observations of social phenomena in populations of the beach mouse (*Peromyscus polionotus leucocephalus*) on Santa Rosa Island, Florida, are presented in the present report. This beach mouse was selected for investigation, because geographic variation and speciation have been recently studied in this species and because the species occurs in an environment that is suitable for a field study of this type. The ecologic community in which this species occurs on Santa Rosa Island is a simple one in regard to its mammalian components. The sparse vegetational cover and sandy soil permitted the location of homesites and the tracking of individual mice.

The field work on which the present report is based was carried on between November 5, 1941, and January 13, 1942, and between May 7 and June 17, 1942.

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METHODS

The field techniques were designed to show the resident population of beach mice, the social organization of the population, and the interrelationships of individual mice with their environment. The field work centered around a live-trapping and marking operation that was designed to mark and record, for the period of the study, all of the beach mice living on a measured segment of Santa Rosa Island. This segment, comprising approximately 65 acres, was staked out in a grid pattern (Fig. 1) for the setting of live traps. The gridded area extended completely across the island, from the Gulf beach to Santa Rosa Sound, and a distance of 560 yards on the long axis of the island. Estimates of population density were based on captures within this 65-acre gridded area. Some traps were set as far as 230 yards to the west of the gridded area, and some were set as far as 480 yards to the east of it, but no attempt was made to capture all of the beach mice in these border areas. The entire area of the study was nearly three-fourths of a mile long.

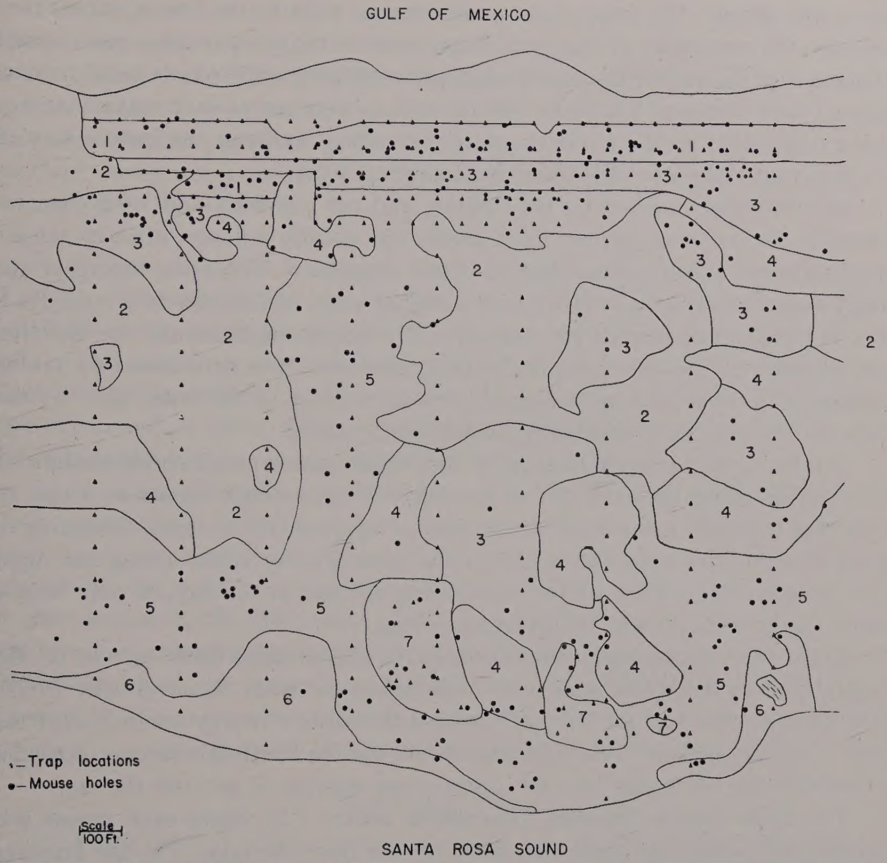

FIG. 1. Plot on Santa Rosa Island, Florida, on which beach mice (*Peromyscus polionotus leucocephalus*) were studied by live-trapping, showing location of traps, location of holes used by the mice, and approximate distribution of vegetation types. Vegetation types are indicated by numerals as follows: (1) Beach Dune, (2) Flood Basin, (3) Sea Oats Interior Dune, (4) Vegetated Flood Basin, (5) Bluestem Interior Dune, (6) Sedge Marsh, (7) Scrub Dune. Note concentration of mouse holes in favorable vegetation types Nos. 1, 3, 5, and 7, and scarcity of holes in unfavorable types Nos. 2, 4 and 6.

The grid stakes over most of the plot were placed 80 feet apart in lines that were 210 feet apart (Fig. 1), but in the dunes facing the Gulf beach the stakes were placed 60 feet apart. Traps were never set at the same time at all of the stakes on the plot. Various combinations of trap settings were used instead, to minimize the localization of mouse movements by the development of a trap habit or by repeated captures near the home site. The traps were sometimes set on the western half of the plot, then on the eastern half; on the northern half, then on the southern half; and in alternating lines with the traps set in the even-numbered lines for a period of days, then in the odd-numbered lines for a like period. The traps were sometimes set only in the beach dunes, then set over the remainder of the plot. Every part of the 65-acre area was trapped at some time during each 2-week period into which the trap records were divided. From 1 to 3 standard live traps (Blair, 1941*a*) were set at each stake that was being trapped. If a mouse was caught 2 succeeding nights at the same stake, all traps at that stake were left unset the following night.

All mice were marked by toe-clipping and ear-punching and were then released at the point of capture. Each mouse was usually followed after its release until it found a hole or was lost in dense vegetation. The open nature of the vegetational cover made it fairly easy to follow most of the mice to a hole. Each hole to which a mouse went was marked with a numbered stake, and the direction and distance of the hole from the nearest grid stake was determined by taking compass directions and by pacing the distance. Most of the holes used by the mice on the plot were eventually marked with stakes.

Tracks in the loose white sand of the island gave a considerable amount of information about the activities of the mice. When a single mouse or a pair of mice was regularly using a particular hole, it was possible to learn something of a night's activities from the tracks in the sand. Tracks made during the night were usually blown away by the wind before the end of the day, so only freshly made tracks were present on a given morning.

Traps were occasionally set at previously staked holes both on and off the central plot to determine what mice were using the holes. A screen-wire tunnel was devised to fit over the hole and prevent the capture of any mouse except the one or ones in the hole. This hole-trap device was used with fair success, but mice sometimes dug their way into the tunnel from outside to get into the trap.

The daily records included information about: (1) where each mouse was caught; (2) where the mice went after release from the trap; (3) the breeding condition of each mouse; and (4) various observations on behavior, social relations, track records, foods, and predators. These more elaborate trapping techniques gave far more information about the beach-mouse population than would have been obtained by simply live-trapping and marking the mice.

ENVIRONMENT OF THE AREA

Climate

Weather records of 51 years at Pensacola, on the coast about 25 miles west of the study area, are representative of the coastal climate in this part of Florida. The climate is warm (average annual temperature of 67.7°F.), moist (average annual rainfall of 57.55 inches), and humid (average 8 A.M. relative humidity of between 78 and 83 per cent). The growing season is long. There is an average frost-free season of 287 days. January is the coldest month, with an average daily maximum of 60.1°F. and an average daily minimum of 45.7°F. August is the warmest month, with an average daily maximum of 87.0°F. and an average daily minimum of 74.6°F.

Temperatures usually drop to or below 32°F. at least once during the year. The average number of days on which the temperature drops to 32°F. or below is 3 for January and 2 for both December and February. Cold waves are usually of short duration, and freezing temperatures are rare on more than 3 consecutive days. Freezing temperatures usually occur with clear weather, and even during the cold waves temperatures rise above freezing during the day.

Soil

Santa Rosa Island is a narrow barrier island of dazzling white sand. The sand is so white that it has the appearance of newly fallen snow. Broken shell fragments occur sparingly throughout the sand. Measurement of the shade of color of this sand with a Photovolt photoelectric reflection meter gives an average value of 62.6 for reflected red, of 58.2 for reflected green, and 53.6 for reflected blue. These values are in terms of percentage of reflectance by comparison with the reflectance from a white magnesium carbonate block.

A line of low barrier dunes (double in some places) parallels the Gulf beach. These dunes result from the action of prevailing onshore winds on the loose beach sands cast up by wave action. This line is broken in places where waves have broken through during storms to flood the interior of the island. The effects of wind action on the loose sand are evident everywhere on the island. Dune and blowout structures are common. Some of the larger dunes near the inner side of the island rise more than 30 feet above the general level of the island. There is little or no accumulation of organic material in the soil except in low marshy areas along the side of the island adjacent to Santa Rosa Sound.

Vegetation Types

The plant cover is scanty over most of the area of the island. Exceptions to this are in the more or less densely grassed beach dunes, in the thickets of woody plants on some dunes near the Santa Rosa Sound side of the island, and in the low sedge marshes adjacent to the sound. Seven vegetational types or microhabitats, are distinguishable in the area studied, in addition to the Gulf beach. These have been mapped (Fig. 1) and are described in some detail.

BEACH DUNE.—The single or double row of low dunes which parallel the Gulf beach and have a more or less dense growth of grasses and other plants. In many places the crests of the dunes have a dense cover of bluestem (*Andropogon maritimus*), which effectively binds the dunes. This grass and *Cyperus lecontei* and *Juncus scirpoides* form a dense cover on some of the low areas between the dunes. The relatively luxuriant growth of grasses in these places presumably results from the water supplied by spray from the surf. Small blowouts are present on some dunes. Sea oats (*Uniola laxa*) grow on the crests and sides of some dunes. Other plants identified include *Iva imbricata, Panicum amaratum, Raimannia humifusa, Chamaesyce ingallsii,* and *Chrysopsis trichophylla.* The beach dunes provide excellent food and cover for small mammals.

FLOOD BASIN.—Shallow depressions in the interior of the island are flooded during heavy or prolonged rains or when excessively high waves break through passes in the beach barrier dunes during storms. These depressions are virtually without vegetation. They offer little or no food or cover for small mammals.

VEGETATED FLOOD BASIN.—Some shallow depressions on the island support a scant number of plants. Like the flood basins, these areas are inundated at times by standing water. A coarse panic grass (*Panicum amaralum*) occurs sparingly, and a small, prostrate spurge (*Chamaesyce ingallsii*) forms a little ground cover. These basins provide very little food or cover for small mammals.

SEA OATS INTERIOR DUNE.—Many low dunes, usually raised less than 3 or 4 feet above the general level of the island, occur in the interior. Some are extensive dunes with the long axis parallel to, at right angles to, or otherwise related to the prevailing wind direction. Others are small isolated dunes bound by a single clump of sea oats or other sand-binding plant. The sand in these dunes is frequently shifted by wind, and blowouts are common. Sea oats is the most common dune builder in some areas. There is usually a scattered open cover of *Andropogon maritimus*. Other important sand-binding plants are *Iva imbricata* and *Odontonychia erecta*. Other plants identified from these dunes include *Panicum amaralum, Chrysopsis trichophylla, Raimannia humifusa, Chrysoma pauciflosculosa,* and *Conradina puberula*. There is an excellent food supply for small mammals on these dunes, but the cover is inferior to that of the beach dunes.

BLUESTEM INTERIOR DUNE.—Some of the interior dunes have a comparatively heavy cover of *Andropogon maritimus*. These dunes are better stabilized than are the sea oats interior dunes, which have an open cover of *Andropogon* and *Uniola laxa*. The relatively stable bluestem dunes are most common on the side of the island adjacent to the sound. Some sea oats occurs on them. Abundant plants include *Chrysopsis trichophylla, Raimannia humifusa, Panicum portoricense,* and *Lachnocaulon engleri*. Other plants are *Iva imbricata, Panicum amaralum, Odontonychia erecta, Spartina patens,* and *Cyperus lecontei*. These dunes are probably slightly inferior to the beach dunes in food and cover for small mammals.

SCRUB DUNE.—The highest dunes in the area studied are close to the sound side of the island. One of these dunes extends over 30 feet above the general level of the island, and all of them are considerably higher than are the dunes discussed above. The sand of these dunes is bound by various species of woody and non-woody plants. Large blowouts are conspicuous on the sides of most of them. Two oaks (*Quercus virginiana* and *Quercus geminata*) form dense, low thickets on the crests and sides of the dunes. Other conspicuous woody plants include *Magnolia grandiflora, Bumelia rufotomentosa, Crataegus lacrimata, Ilex vomitoria, Pinus caribaea,* and *Callicarpa americana*. The woody vegetation has a scrubby appearance, as seldom more than 6 or 8 feet of the trunks are exposed above the sand. Clumps of *Andropogon maritimus* occur here and there is some sea oats. Some common herbs and grasses include *Panicum portoricense, Rumex hastatulus, Galium bermudense, Froelichia floridana,* and *Galactium* species. Other plants are *Panicum amaralum, Toxicodendron radicans, Cuscuta* species, *Ceratiola ericoides, Tradescantia reflexa, Odontonychia erecta, Chrysoma pauciflosculosa, Delopyrum* species, and *Chrysopsis trichophylla.* These dunes have abundant food for small mammals. The cover is good, but it is not as continuous as in the beach dunes.

SEDGE MARSH.—Low areas of the island adjacent to Santa Rosa Sound are more or less flooded during heavy rains, during high tides in the sound, or when there are strong offshore winds. These areas remain muddy most of the time, and in places there are permanent tidal pools. There is a well-developed salt marsh in these areas. Organic detritus has accumulated here to form a dark marsh soil which contrasts strongly with the white sand of the remainder of the island. The heavy grass and sedge cover is made up principally of *Spartina patens, Andropogon virginicus,* and *Eragrostis elliottii.* There is a small amount of *Andropogon maritimus* scattered through the area. Other plants include *Fuirena scirpoidea, Setaria geniculata, Sabbatia campanulata, Centella repanda, Hydrocotyle bonariensis, Gyrotheca tinctoria, Solidago petiolata,* and *Solidago mexicana.* The only woody plant is *Baccharis halimifolia,* which is scarce and scattered. Beach mice were taken rarely in even the edges of the sedge marshes, but the cotton rat (*Sigmodon hispidus*) was only taken in these marshes.

GULF BEACH.—The Gulf beach, seaward of the beach dunes, is devoid of vegetation. The sand is in a constant process of change due to wave and wind action. There is no cover and there are no homesites for beach mice. Animal foods and some plant foods are available in the detritus cast up by the waves.

POPULATION NUMBERS, DENSITY, AND STRUCTURE

A measure of population size, density, and structure was obtained by live-trapping and marking the beach mice on the central plot. For purposes of analysis, the trap records are broken down into 2-week units. The total catch of beach mice during each 2-week period is considered, therefore, to be an estimate of the total beach-mouse population of the plot, exclusive of young in the nest, for that period. Five such 2-week periods are included in the fall-winter work of 1941-42, and 3 are included in the spring work of 1942.

Numbers of Mice Caught

The total number of beach mice caught on the central plot varied from a low of 69, in the first 2 weeks, November 5 to 18, 1941, to a high of 117, in the

TABLE I

Beach Mice of Different Sex, Age, and Residence Classes
Trapped on 65.08 Acre Plot on Santa Rosa Island, Florida

Period	Adult Female		Adult Male		Immature Female		Immature Male		Total Resident Adults	Totals
	Resident	Transient	Resident	Transient	Resident	Transient	Resident	Transient		
Fall-Winter										
Nov. 5-18, 1941	17	4	24	6	5	11	..	2	41	69
Nov. 19-Dec. 2, 1941	26	1	32	8	2	6	4	1	58	80
Dec. 3-16, 1941	26	3	34	5	6	4	1	3	60	82
Dec. 17-30, 1941	31	4	39	5	13	15	3	7	70	117
Dec. 31, 1941-Jan. 13, 1942	32	1	30	3	5	8	..	8	62	87
Spring										
May 7-20, 1942	22	4	53	4	4	1	3	2	75	93
May 21-June 3, 1942	24	..	53	1	1	..	1	..	77	80
June 4-17, 1942	24	3	40	5	..	..	..	..	64	72

weeks of December 17 to 30 (Table I). One might be led to assume that the increase from the comparatively small catch during the first 2 weeks indicates a considerable effect of the trap technique on the number of animals in the area. Thus, it might be thought either that the presence of an abundance of exotic foods in the traps had drawn transient animals to the area and increased the number of resident mice, or that the development of a trap habit had led to the capture of a larger proportion of the population, after the residents became accustomed to going to the traps for food. Both of these factors may be discounted, because the spring trapping, after a lapse of nearly 4 months, recorded a catch for the first 2-week period greater than that of either of the following periods. Most of the mice trapped in the first spring period were unmarked individuals that had not been living on the plot during the earlier trapping. The small catch in the first 2 weeks of the fall trapping probably indicates a comparatively low population level at that time. There was a gradual increase in numbers to the peak in late December. Remarkably little variation in total numbers of beach mice occurred in the spring period (Table I).

Sex, Age, and Residence Classes

The total beach-mouse population may be broken down for analysis into age classes, sex classes, and classes of resident as opposed to transient individuals (Table I). Any animal that was sexually mature was considered an adult regardless of age or pelage. Males and females that from their pelage and size could not have been more than 6 or 7 weeks old were sexually active and were considered adults. Animals that showed by their size and appearance that they were older than the minimum breeding age were also classed as adults. Any mouse that was taken 4 or more times on the plot was classed as a resident, the rest as transients. This division is arbitrary, but there is evidence that it did separate most of the resident from the transient animals. In the first 3 weeks of trapping in the fall, 138 beach mice were recorded on the plot. Twenty-seven of these were never caught more than once, 15 never more than twice, and 13 never more than 3 times. There is an abrupt break in the frequency curve at 4 captures, with only 3 mice caught 4 times, and the curve is relatively flat beyond this point.

In the case of wandering individuals, it is to be expected that the number of individuals in the record would vary in inverse proportion to the number of captures. More transients would be caught once than would be caught twice. The rather flat curve in the case of the resident mice probably results from a continuing process of change in the resident population. Some of the transient mice settled on the plot and consequently are treated as residents, while other mice were resident on the area during the entire time. Of the 15 mice caught only twice, 5 were caught on consecutive nights, 4 were caught 2 nights apart, and 2 were caught 3 nights apart. There seems little question but that these were transients that paused for a short time, then moved on. One was caught 10 nights apart, and one was caught 11 nights apart. While these last are classed as transients, it is impossible to eliminate the possibility that they had established themselves only to be taken by predators. Of the mice caught only 3 times, three were taken 4 nights apart; one, 7 nights; one, 8; one, 13; and one, 17 nights apart. While these are classed as transients, we cannot be sure that some of them did not establish residence.

Resident Breeding Population

The resident breeding population, the genetically important section of the total population, fluctuated less from period to period than did the total population (Table I). Yet a gradual increase in the number of resident adults was noted from early November to a peak in late December, followed by a drop in early January. The spring population of resident adults fluctuated a little at a level somewhat above the average number for fall.

The sex ratio in the resident adult population showed some interesting variation. Fluctuations from the expected 1:1 ratio of males to females were slight during the fall-winter period, and all deviations are well within the limits of sampling error. In the first 2 trapping periods of spring, resident males significantly outnumbered resident females. In the period of May 7 to 20, there were only 22 females to 53 males. The chi-square value for the deviation from the expected 1:1 ratio is 12.81, which is highly significant. In the following 2 weeks, males outnumbered females by 53 to 24. The chi-square value for this deviation is 10.92, which is highly significant. An adjustment of the sex ratio occurred by the time of the next 2-week period owing to the disappearance of 13 males and an increase of 1 in the number of resident females. The chi-square value for the deviation of the 24:40 ratio from the expected 1:1 ratio is only 4.00, which is not significant to the 1 per cent level. The unbalanced sex ratio in the resident mice in May cannot be explained on present evidence. It is noteworthy that the adjustment of the sex ratio toward a balanced number of males and females came about largely through the disappearance of excess males rather than by the settlement of additional females. The excess males may have moved out of the area.

Juvenile Mice

Juvenile mice comprised at least a small fraction of the total population in every trap period (Table I). The greatest number occurred in the period of December 17 to 30, when 38 were recorded. In this period juveniles comprised 32.5 per cent of the total mice recorded. Only 16 of these became residents; 22 were transients. The least number of juveniles present in the fall-winter period was in the period of November 19 to December 2, when 13 (16.2 per cent of the total population) were recorded. In the other fall-winter periods, juveniles comprised from 17.1 to 26.1 per cent of the total number of beach mice recorded. A very different situation existed in the spring period: May 7 to 20, 10 juveniles comprised 10.7 per cent of the total population; May 21 to June 3, 2 immatures made up only 2.5 per cent of the population; and June 4 to 17, no juvenile was recorded. It is evident that much breeding activity took place in November, December, and early January. It is also evident that little breeding activity occurred during May and early June.

Population Density

Population density is expressed as the average number of individuals per acre. The central plot comprised 65 acres. The north and south boundaries of the plot were, respectively, Santa Rosa Sound and the Gulf of Mexico. To the east and west, no barriers to the movement of the beach mice were present at the boundaries of the plot. Before population densities may be calculated, therefore, the area trapped must be corrected to allow for animals taken on the plot whose ranges extended beyond the area on which traps were set. This correction is made by adding one half the width of an average home range to each side not delimited by a barrier to the species (Blair, 1940). The corrected trapping area for the beach mice is 83.08 acres.

The population density of beach mice fluctuated in the neighborhood of one individual per acre (Table II). The least density was in the period of November 5 to 18, when there was an average of 0.82 individuals of all categories per acre. The greatest density was in the period of December 17 to 30, when there was an average of 1.40 individuals per acre. The only other estimate of population densities of beach mice is that given for another subspecies of *Peromyscus polionotus* in sand scrub near Lake Placid, Florida (Rand and Host, 1942).

TABLE II

Average Population Density of Beach Mice (*Peromyscus polionotus leucocephalus*) Per Acre

Date	Estimated Resident Females Per Acre	Estimated Resident Males Per Acre	Estimated Juvenile and Transient Females Per Acre	Estimated Juvenile and Transient Males Per Acre	Estimated Total Per Acre
Nov. 5-18, 1941	0.20	0.29	0.24	0.10	0.83
Nov. 19-Dec. 2, 1941	0.31	0.39	0.11	0.16	0.97
Dec. 3-16, 1941	0.31	0.41	0.16	0.11	0.99
Dec. 17-30, 1941	0.37	0.47	0.39	0.18	1.41
Dec. 31, 1941 -Jan. 13, 1942	0.39	0.36	0.17	0.13	1.05
May 7-20, 1942	0.26	0.64	0.11	0.11	1.12
May 21-June 3, 1942	0.29	0.64	0.01	0.02	0.96
June 4-17, 1942	0.29	0.48	0.04	0.06	0.87

These workers dug the mice from their burrows on 2-acre and 3-acre plots and estimated the population per acre from the numbers of mice found in the burrows. They estimated as many as 7.90 individuals per acre. They did not correct for the extension of ranges of the mice beyond the study plots, and they consequently arrived at apparently excessively high estimates of population density. If it is assumed that the home ranges of mice of the subspecies *leucocephalus* are representative of home-range size of other populations of the species, their data can be corrected for the extension of ranges beyond the plots. If one half the width of an average *leucocephalus* home range is added around the periphery of their 3-acre plots, the size of the area from which the mice were taken now becomes 18.57 instead of 3 acres. In the overgrown field habitat studied by Rand and Host, the corrected estimate of the number of mice per acre becomes 0.93 instead of 5.77 individuals per acre. In their sandy overgrown roadbed, bordered by scrub, the corrected estimate is 1.35 instead of 8.33 individuals per acre. It is noteworthy that the corrected estimates for the density of population of mice of the subspecies *phasma* in southern Florida approximate rather closely the estimates for *leucocephalus* on Santa Rosa Island. Rand and Host's counts included all young in the nest regardless of age.

Concentrations of Mice

The best estimate of the crowding or lack of crowding in a population is the estimate of concentration based on the average number of resident individuals of a species per average home-range area (Blair, 1941*b*). The number of average home-range areas afforded by the area being trapped is determined and then is used as the divisor of the number of individuals recorded from the area to determine the number per home range area. A concentration of less than 1 individual per available home-range area indicates barren or nonoccupied areas on the plot. A concentration of 1 individual per home-range area might indicate territorial behavior, with no barren spots and with the range of each individual meeting and stopping at the limits of the range of adjoining individuals, or it might indicate overlapping ranges in some parts of the area with barren spots in others. A concentration of more than 1 individual per home-range area indicates overlapping of ranges. The greater the increase in concentration value the greater is the amount of overlapping of home ranges and the greater is the presumed amount of competition for food, homes, and mates.

The area from which beach mice were being trapped afforded 12.51 average home-range areas for males and the same number for females. Concentration values for both sexes are listed in Table III. Males were notably more crowded than females in both the fall-winter and spring periods. Even at the period of least concentration of males in early November, there was an average of 1.92 individuals per average home-range area. The greatest concentration of males occurred in the 2 May periods, when there was an average of 4.24 resident males per home-range area. Females were least crowded in early November, when there was an average of only 1.36 females per home-range area. They were most crowded in late December, when there was an average of 2.56 individuals per home-range area. The less crowded condition of the females probably resulted from greater antagonism between females than between males. Additional evidence will be presented later concerning antagonism between females.

TABLE III

CONCENTRATIONS OF RESIDENT BEACH MICE IN TERMS OF ESTIMATED NUMBER OF INDIVIDUALS PER AVERAGE HOME-RANGE AREA

Period	Resident Males		Resident Females	
	Number	Number Per Average Home-range Area	Number	Number Per Average Home-range Area
Fall-Winter				
Nov. 5-18, 1941	24	1.92	17	1.36
Nov. 19-Dec. 2, 1941	32	2.56	26	2.08
Dec. 3-16, 1941	34	2.72	26	2.08
Dec. 17-30, 1941	39	3.12	31	2.48
Dec. 31, 1941-Jan. 13, 1942	30	2.40	32	2.56
Spring				
May 7-20, 1942	53	4.24	22	1.76
May 21-June 3, 1942	53	4.24	24	1.92
June 4-17, 1942	40	3.20	24	1.92

Population Size

The total size of the population of *leucocephalus* on Santa Rosa Island has been estimated from the data obtained in this study (Blair, 1946). This geographically isolated population is well differentiated from mainland populations of *polionotus*. It apparently represents a stage in speciation short of, but approaching, differentiation into a separate species. The total population size is, therefore, of considerable interest. Estimates (Blair, 1946) place the total population size between about 10,000 and about 17,600 during the period of field work. Reductions in population size much below these levels doubtless occur when the island is swept by hurricanes.

POPULATION CHANGES

The composition of the population of beach mice on the study area was continually changing throughout the period of field work. This condition of flux is not brought out adequately by the estimates of population numbers and population density. The total number of individuals might remain essentially the same from one period to the next, but there was always some change in the individuals themselves. Population changes resulted from: (1) the death or disappearance of a resident animal, (2) the movement of maturing young animals away from the area, (3) the appearance of immature mice that were either born there or that moved there from other areas, (4) the appearance of transient or immigrant adults, and (5) the sexual maturation and establishment of residence by juvenile mice. The population is here considered from the viewpoint of the changes that took place in its composition during the course of the work. The field project was designed primarily for a study of the nature of the beach-mouse home range rather than for a study of changes in the population and was, therefore, of too short duration to give an adequate measure of population changes, but it does provide some worthwhile information about them.

Some resident mice disappeared from the plot in each 2-week period (Table IX). A mouse was considered to have disappeared in the last 2-week period in which it was recorded. No determination of losses can be made for the last period of fall or for the last period of spring. Forty resident beach mice disappeared from the plot during the fall. Eight of these are known to have died as a result of being trapped, for 5 died of cold in the traps, 1 drowned in a trap during a storm, 1 died in a trap accidentally left set, and 1 died in an epileptic seizure as it was being handled. Five mice that disappeared from the plot record in the last December period lived on the margin of the plot and 1 of them remained resident there outside the plot until spring. Absence of these 5 animals from the plot record for the 2-week January period simply indicates that they were not taken in that time on the part of their respective home ranges that extended onto the edge of the plot. There is no certainty about the fate of 27 of the resident mice that disappeared during the fall. Most of them probably died or were taken by a predator. None of them were taken in extensive trapping beyond the limits of the plot. Movement away from the plot would have been limited to only two directions, as the plot extended completely across the narrow island. Failure to recover any of the mice in either direction suggests that their disappearance was due to death. There is a suspicion that some of the deaths that are unaccounted for may have resulted indirectly from the trapping. The number of disappearances was greatest during the cold month of December. If there was any cumulative, deleterious effect from spending the night in a trap during cold weather, this might account for the apparent increase in deaths of residents during the cold weather. Some of the missing mice may have been taken by shrikes (*Lanius ludovicianus*), after release from the traps. These birds followed me boldly and attempted to catch the mice after they were released. They are known to have taken at least 2 mice in spite of my efforts to frighten them away. One mouse captured was a female that was considered a transient, but the other was a resident male taken January 10. Probably, some of the mice that did not go directly to their nest after release were picked up by shrikes after I left the area. Four of the 27 mice that disappeared without a clue in the fall period found no hole after release on the last morning of capture, and these were possibly caught by shrikes.

Twenty-one resident beach mice disappeared from the plot records in the spring period. Five of these were accounted for by the fact that their home ranges barely overlapped the central plot, and their absence from the plot records did not indicate disappearance from the area. All were caught adjacent to the boundaries of the plot after they had disappeared from the plot record. Sixteen of the 21, however, disappeared without a clue to the cause for their loss. No mice had died in the traps, and shrikes did not bother the mice in the spring. With the great excess of males over females in the spring, it is possible that some of the lost males moved away. None of the 16 mice was recovered away from the plot, however, and there is no certainty that the loss of these animals was not due to their death.

Movements were common among the young mice that had not yet reached sexual maturity or that were just becoming sexually mature. These young mice appeared to wander for a time after leaving the nest; then as they became sexually active they usually settled down and remained in a particular area. This phenomenon has been reported in other species of *Peromyscus* (Blair, 1940; Burt, 1940; Howard, 1949). Fourteen immature beach mice moved from the place they were first caught and settled within the limits of the trapping efforts. The minimum distance of movement was 980 feet. The maximum was 1970 feet. The average distance of movement of these 14 mice was 1415±89 feet. There is no certainty that these values represent the total distances of movement, for there is no certainty that an immature mouse was first taken in the vicinity of the nest in which it was born. These mice might have been caught near the nests in which they were born, or they might have been making dispersal movements across the plot when they were first caught. The known distances of movement of these mice nevertheless give an indication of the minimum distances the young might move in dispersing away from the nest.

Dispersal movements by young mice and the establishment of residence by them accounted for the great bulk of the changes in the beach-mouse population.

Sixty-one (88.4 per cent) of the 69 mice that appeared on the plot and also became residents in the fall were young mice that looked to be from 3 to 6 weeks of age when they were first caught. Only 8 (11.6 per cent) of the 69 mice were fully grown. In the spring, 8 (72.7 per cent) of the 11 mice that settled on the plot, after the first 2 weeks of trapping had revealed the resident population, were young, and only 3 (27.3 per cent) were grown. Among the 92 transient mice that did not settle on the plot in the fall, 77 (83.7 per cent) were young mice, and only 15 (16.9 per cent) were mature in size. Of 19 transient mice in the spring, 12 (63.2 per cent) were young individuals, and 7 (36.8 per cent) were fully grown.

The resident population of beach mice on the plot was augmented, and the loss of resident individuals counterbalanced, by (1) maturation of young mice that had appeared in a previous period as immature, nonbreeding animals; (2) settlement of young, sexually active mice that had presumably dispersed from their point of birth beyond the limits of the plot; and (3) the appearance of a few fully grown, breeding individuals. All of these sources of new individuals were factors in maintaining and increasing the population (Table IX). The resident population in the fall built up to a peak in late December (Table I), because the rate of maturation and immigration of young mice exceeded the rate of loss of residents (Table IX). In the spring, which was a period of little reproductive activity, the resident population declined, because the loss of residents was not balanced by the appearance of maturing young. The sudden appearance of fully grown mice after the plot had been trapped for a considerable period was sometimes difficult to understand. Five of 11 fully grown mice that appeared were residents on adjacent areas with home ranges that overlapped the plot to some extent. Failure to take these mice earlier presumably resulted from the fact that only a fraction of the home range extended on the plot. Six of the 11 were never taken in border areas, and they may have been genuine immigrants that had changed their home range from some other area. That these were really immigrants rather than nearby residents is believed to be the case, because the known home range of only one of them reached to the border of the study plot. One settled midway of the plot in the beach dunes and the range of none of the other four extended near the outer lines of traps.

Little can be said about the events that take place during the settlement of a mouse in an area. The animal must either dig a hole or a series of holes, as do the beach mice, or take over a hole or series of holes occupied or abandoned by another mouse. It must locate a supply of food, and it will presumably become associated with a mouse of the opposite sex. Acquisition of a home may conceivably be a major problem for a mouse attempting to settle in a densely populated area. This did not seem to be the case with the beach mice, for these mice utilized a variety of holes, including holes that had been made by their predecessors in the population. They were also adept at digging a new hole when necessary. There were a few indications that a beach mouse might sometimes have difficulty in settling in a well-populated area. Three of the young mice that appeared on the plot appeared to have been in fights. An immature male had numerous wounds on its back, and a transient young adult male had a lame foot. A transient young adult female had a torn ear. Fighting was observed a few times between residents and transients or immigrants. A transient young adult male was first discovered on the plot, when a resident female went to a hole after release and chased this male out. This male was trapped the following night, but it was never taken again. On 3 occasions immature or young, sexually mature females went from the traps to holes from which they were subsequently chased by resident females who went there shortly after them. Two of the young females settled on the plot; 1 did not. On 1 occasion a resident male went into a hole, and nothing happened to indicate that the hole was already occupied. A resident female that associated regularly with this male went there a few minutes later and evicted a transient, immature female. On 1 occasion a transient, sexually mature male went, after its release, to a hole into which a resident male had gone a few minutes earlier. The resident male drove the transient male out of the hole. These observations, scanty though they may be, point to conflicts between resident beach mice and immigrant mice that may attempt to establish residence in the area.

Unset traps afforded a temporary home for some of the transient and immigrant mice. The traps were overturned so that the door was open, when the traps were not being run on a particular part of the plot. Since the traps contained cotton nesting material, they provided an adequate home. No mice attempted to live in unset traps during the spring, presumably because the traps became too hot during the day at that time of the year. But in the fall-winter period 18 mice were noted living in unset traps. In 10 of these cases, discovery in an unset trap gave the first indication of the presence of the mouse on the plot. In 5 instances, each of the mice was found in an unset trap, after having been caught once on the plot; 1 mouse after having been caught twice; 1 after having been caught 4 times; and 1 after having been trapped 9 times. Thirteen of the 18 mice were or became residents on the plot. Five were transients. The unset traps obviously provided temporary homes for mice that had not yet established themselves in the area. An immigrant immature female and an immigrant young, sexually mature male were first recorded on the plot, when they were discovered living together in an unset trap. This pair became residents on the plot.

The rate of turnover in the beach-mouse population is indicated by the number of individuals that remained on the plot from the fall to the spring period of trapping. Seventeen (19.5 per cent) of the 87 beach mice recorded on the plot in the period of December 31 to January 13 were still present about 4 months later, in the period of May 7 to 20. Thus 81.5 per cent of the beach-mouse population of the plot was lost in the 4-month period. Fourteen of the 17 mice that survived to spring were members of the resident, breeding population in January. One of these was a young adult immigrant, and 2 were immature mice. The 17 mice that survived from January to May comprised 17.2 per cent of the total population of the plot in the spring period. The turnover in the beach-mouse population was estimated to be of the same order of magnitude as that in closely related species of *Peromyscus* (Blair, 1948).

HOME RANGES

Estimates of home-range size obtained from live-trapping and marking data are highly useful in estimating the theoretical rate of spread of characters through a population and are essential in such phases of applied biology as wildlife management and the control of disease vectors. Methods of estimating home-range size from trap data vary considerably among different recent workers (see Hayne, 1949). In the present study data from live-trapping and marking beach mice are examined with respect to what they may show about the nature of the home ranges of these mammals and the reliability of home-range size estimates made from trap data. The data include: (1) place records of the capture of individual mice in live traps; (2) records of tracking of individual mice in the sand of Santa Rosa Island; (3) records of refuge holes and den holes available to and used by the mice; and (4) records of the behavior of mice after release from the traps.

Estimation of Home-range Size from Trap Records

The grid pattern of the traps, the spacing of the traps, and the types of data recorded have already been discussed. Estimates of the home range of each mouse which was caught 10 or more times, were made from the trap data by the same methods employed in previous studies (Blair, 1940). The outermost traps in which a mouse was caught were used to establish the limits of the estimated home range, with the limits of the range lying halfway between the outermost points of capture and the next adjacent traps. The records of individuals caught less than 10 times were arbitrarily excluded as probably incomplete, which minimized the bias introduced by unequal completeness of observations on individuals. The use of records of mice caught 10 or more times follows the precedent of Haugen (1942) and Blair (1942), who noted that enlargement of the estimated range with additional captures slowed or ceased in certain species after about this number of captures. The length of the periods of observation, on which estimates of home-range size were made, are rather longer than in my previous studies. The estimates of the fall ranges were made from data collected between November 5, 1941, and January 13, 1942. The estimates of the spring ranges were made from observations between May 7 and June 17, 1942. Although the fall period (10 weeks) was greater than the spring period (6 weeks), the average number of captures was very close for the 2 periods (Table IV). One objection to estimates of home-range size from data collected over such long periods of time is the possibility that an animal may partly shift its range or move entirely away. Actually, the few changes of range which occurred were evident in the raw data, and the area occupied after any such movement was excluded from the home-range estimate. The major advantage of this longer period over the "trap-month" used by myself and others is that all of the trap-record data available are utilized in estimating the home range of each mouse. The estimated home range based on records of capture was called the "trap range."

TABLE IV

AVERAGE SIZE (IN ACRES) OF ESTIMATED HOME RANGES OF BEACH MICE (*Peromyscus polionotus leucocephalus*) DETERMINED FROM TRAP RECORDS
Data for males and females are combined.

Sample	Number of Individuals	Average Number of Captures	Average Size of Trap Range in Acres
In beach-dune area, Fall, 1941	25	15.84	1.97± .26
In other areas, Fall, 1941	30	15.73	6.38± .81
In beach-dune area, Spring, 1942	28	17.18	5.76± .74
In other areas, Spring, 1942	37	16.38	10.66±1.46

Any one or all of several variables might have contributed to the variation in the size of the trap ranges. The most important of these are sex, type of vegetational environment occupied, and season of the year. No significant differences between the sexes in mean range size were noted under any combination of the other variables, so the trap-range data of males and females have been lumped for consideration of the other factors. Beach mice living in the comparatively dense cover of the dunes fronting the Gulf beach appeared to range less widely than the mice living in the more open cover of the remainder of the study area, so their trap ranges were treated separately. The fall-winter estimates were kept separate from the spring estimates (Table IV).

The trap ranges of the mice living in the more densely covered dunes fronting the Gulf beach averaged significantly smaller than those of the mice living in the more open cover of the middle and northern part of the island (Table IV). In the fall-winter period, the difference in the means for the 2 groups was 4.41±.85 acres. This difference is significant beyond the 1 per cent level of probability. In the spring period the difference in the means was 4.90±1.64 acres. This difference also is significant beyond the 1 per cent point. The smaller average trap range of the mice living in the area of the beach dunes may be explained in part by differences in trap spacing in the two areas (Fig. 1). The stakes to mark trapping points were set only 60 feet apart in the beach-dune area. On the remainder of the plot, the traps were set 80 feet apart in lines that were 210 feet apart. The routine used of trapping on alternating lines, on alternating sectors, or at alternating stakes presumably minimizes in either area any localization of movement of individual mice by the traps. Any bias toward a smaller estimate of range in the beach-dune area would come, therefore, from the mechanics of plotting the home-range area. Since the outer limits of the estimated range are established halfway between the outermost trap in which the mouse was caught and the next outer adjacent trap in which it was not caught, closer spacing of the stakes in the beach-dune area would result in a smaller estimate of the home range. It is realized now that even spacing of all traps on the plot would constitute better technique, since it wouuld eliminate this source of bias.

In order to determine whether or not the apparent differences in average size of range in the two areas resulted from uneven spacing of the traps or from actual differences in range, the maximum distance of capture for each mouse was computed and the two groups compared on this basis. In the beach dunes in the fall, the average maximum distance of capture for the combined males and females was 343.92±40.59 feet. In other parts of the island at the same time, the maximum distance of capture averaged 691.94±54.67 feet. The difference between the 2 means is 348.02±68.09 feet, which is significant beyond the 1 per cent level of probability. Similar results were obtained when we compared mean maximum distances of capture in the spring. In the beach-dunes in the spring the maximum distance of capture averaged 666.07±68.62 feet. In other areas at the same time, the maximum distance of capture averaged 951.08±61.76 feet. The difference between the 2 means is 285.01±92.32 feet, which is significant beyond the 1 per cent point. The comparison of maximum distances of capture does indicate that the mice in the beach-dune area ranged less widely than those in more open areas of the island. Some bias, therefore, in the estimation of home-range size in the two areas cannot be denied, but it is not sufficient to account for the significant differences in size in the 2 types of environments.

The trap ranges of the mice averaged significantly larger in the spring than they did in the fall in both the beach-dune area and in other parts of the island (Table IV). In the beach-dune area the difference between the fall and spring means is 3.69±.78 acres, which is significant beyond the 1 per cent point. In the more open areas the difference between the fall and spring means is 4.28±1.67 acres, which is significant between the 1 and 2 per cent levels of probability.

Although the trap ranges averaged larger in the spring than in the fall, the records of 9 mice that were caught 10 or more times at each season give no evidence of a wider range in the spring. Five of these had larger ranges in the fall than in the spring, and 4 had their largest range in spring. If, as the averages indicate, the mice did range more widely in spring than in the fall the reasons are unknown. A lesser supply of food in the spring and wider ranging in search of food might have been a contributing factor to the larger spring trap range. Such food items as the fruits of the sea oats (*Uniola laxa*), bluestem (*Andropogon maritimus*), and other herbaceous plants were noticeably more plentiful in the fall than in the spring. There was much more breeding activity in the fall than in the spring, and the presence of young in the nest perhaps tended to restrict the wandering of the adults.

Homes Per Home Range

An attempt was made to follow each mouse to a hole after its release from a trap. In some cases the mouse entered dense vegetation and, while it probably entered a hole, it was not possible to locate the hole. In many other cases it was possible to follow the mouse to a hole, and 499 holes were located and charted on the study area. Of this number 325 were located during the fall-winter period and 34 of them were still in use when work was resumed in the spring. An additional 174 holes were located in the spring, making a total of 208 holes located for that period. Mice were followed to holes a total of 1138 times for an average of about 2 records per hole. The holes used were either old holes of the ghost crab (*Ocypoda*), or they were holes that appeared to have been made by the mice themselves. The holes were nearly always located at the base of a shrub or clump of grass or in proximity to some vegetational cover.

Each estimated home range of a beach mouse contained an average of about 20 mouse holes, of which an average of about 5 were entered one or more times by that mouse after its release from the traps (Table V). When released from the trap each resident mouse appeared to be well oriented within its home range and showed little or no hesitation about moving off to one of the available holes. According to the observations (Table V), each mouse had a refuge available in

TABLE V

AVERAGE NUMBER OF MOUSE HOLES PRESENT AND USED PER HOME RANGE OF BEACH MICE ON SANTA ROSA ISLAND, FLORIDA

Sample	Average Number of Holes in Home Range	Average Number of Holes Used	Average Number of Holes Per Acre	Average Number of Holes Used Per Acre
Females				
In beach dunes, Fall-Winter, 1941-42	13.53	3.87	8.35	2.39
In open, Fall-Winter, 1941-42	22.08	5.69	3.72	0.96
In beach dunes, Spring, 1942	22.11	5.00	4.90	0.92
In open, Spring, 1942	29.85	5.61	2.64	0.50
Males				
In beach dunes, Fall-Winter, 1941-42	22.00	5.30	8.80	2.12
In open, Fall-Winter, 1941-42	25.76	5.06	3.31	0.65
In beach dunes, Spring, 1942	19.85	4.95	2.25	0.56
In open, Spring, 1942	20.26	5.48	2.21	0.60

several different parts of its home range. These holes were more than mere refuge holes. A mouse would use one hole for a time, storing food there and nesting there, then similarly utilize other holes within its home range. Captures in "hole traps," designed to catch the mouse emerging from a particular hole without permitting others to be caught, support this conclusion. Likewise, evidences of activity furnished by tracks in the sand indicate regular use of several holes in its range by a beach mouse (see Fig. 2). After a storm had obliterated many of the holes with drifting sand, mouse trails would be seen leading around to the different holes in the home range and the holes would be freshly unplugged. This would seem to be proof that the individual maintains the different holes it utilizes.

The home ranges of these mice differ markedly from the usual concept of a home range, that is one having a single homesite about which the activity of the animal centers, with decreased activity away from the homesite. In the present case, in which several different homesites are utilized, activity may shift from one part of the range to the other, with the behavior of the animal resembling a miniature type of nomadism.

Vegetation Types Within the Home Range

Eight microhabitats, each differing in vegetation and sometimes in soil as well, were described within the study area. These were distributed in a mosaic pattern except for the Gulf Beach and Beach Dune types, which paralleled the open Gulf of Mexico, and the Sedge Marsh, which was distributed along the shore of Santa Rosa Sound (Fig. 1). The frequencies of occurrence of these different vegetation types on the study area and their average frequencies per beach-mouse home range are indicated by percentages in Table VI. In the fall

TABLE VI

Coverage of Different Vegetation Types on Study Area and Their Average Coverage Per Beach-mouse Home Range in the Spring and Fall-winter Periods

Percentages of Cover Types	Beach Dune	Flood Basin	Sea Oats Interior Dune	Vegetated Flood Basin	Bluestem Interior Dune	Sedge Marsh	Scrub Dune	Gulf Beach
On plot	5.9	21.4	18.2	13.8	27.8	5.3	3.7	4.0
Per average home range during fall-winter period	16.4	12.9	16.0	8.8	29.5	3.6	5.3	7.6
Per average home range during spring	7.7	19.1	17.5	12.5	30.9	3.8	5.0	3.4

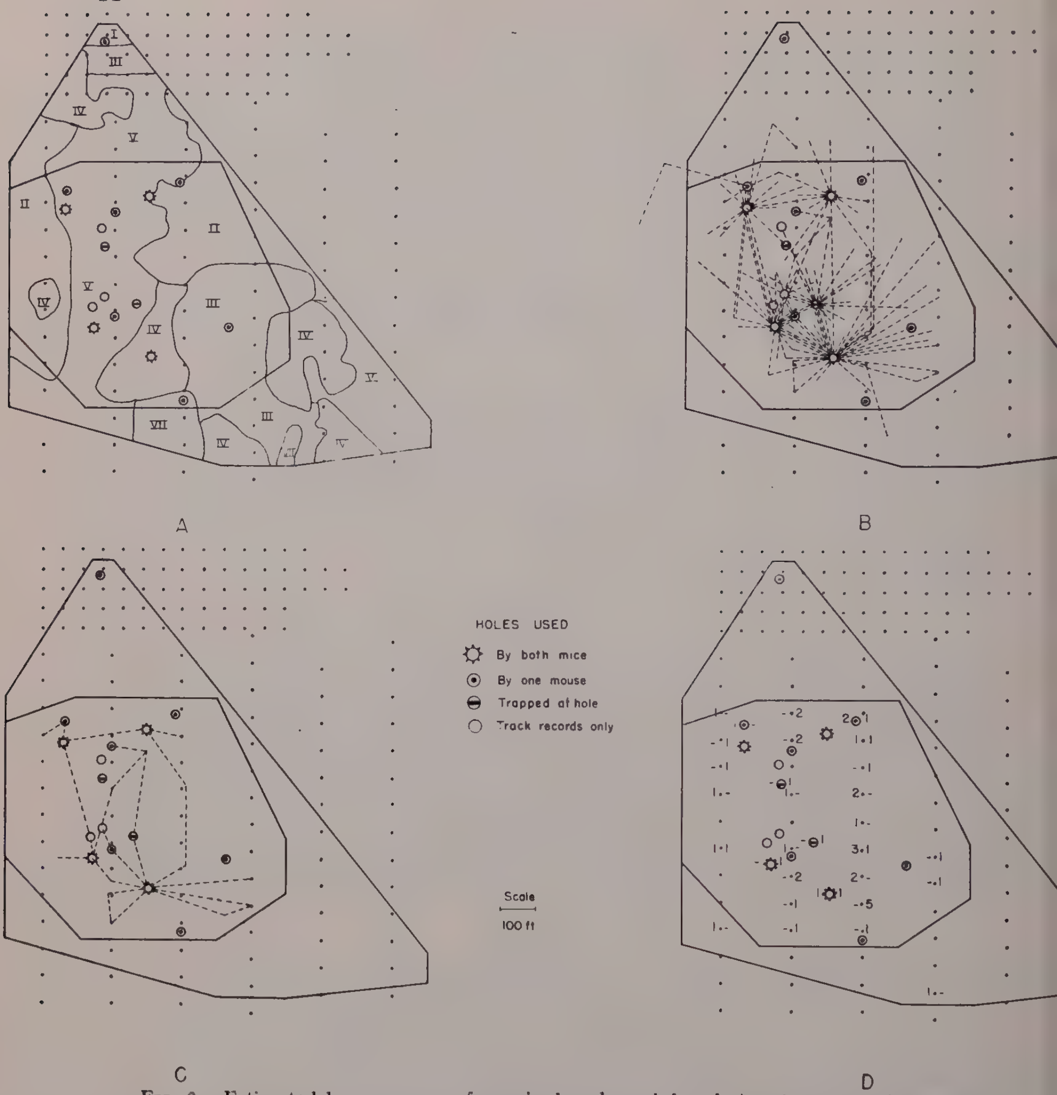

Fig. 2. Estimated home ranges of a paired male and female beach mouse (*Peromyscus polionotus leucocephalus*) in the fall-winter period of 1941-42. Larger trap-estimated range belongs to the female, smaller to the male. Trap locations are indicated by dots.

A. Vegetation types in the home range and holes used by the mice. Roman numerals designating vegetation types correspond to Arabic numerals in Figure 1.

B. Area of activity of the mice as indicated by track records for 10 different mornings. Broken lines indicate direction and greatest distance of trails from holes.

C. Area of activity of the mice on a single night as indicated by track records on the morning of December 15, 1941.

D. Numbers of captures of each mouse of the pair in each trap in the home range. Figure to the reader's left of dot indicating trap pertains to the female; figure to the right pertains to the male.

period the average home range included more of the Beach Dune than would be expected if there was completely random distribution of the home ranges in relation to vegetation types. In this period the average home range included less of the Flood Basin and Vegetated Flood Basin types than would be expected with random distribution of the home ranges. The excess of the Beach Dune type present in the average range results from the excessive concentration of individuals in the beach-dune area at a time of high population density. The mice appeared, in the fall, to avoid the Flood Basin and Vegetated Flood Basin types, in which there was little or no cover and little or no available food. In the spring the frequencies of the various vegetation types in the average home range were very near the frequencies which would be expected with random distribution of the mice in respect to vegetation types.

The Beach Dune, Sea Oats Interior Dune, Bluestem Interior Dune, and Scrub Dune types offered abundant food and cover for the beach mice. The Flood Basin, Vegetated Flood Basin and Gulf Beach types offered little in the way of food or protective cover, and the dense cover and muck soil of the Sedge Marsh type appeared to be avoided by the mice. This latter group might be termed disadvantageous types, of negative value to the mice. The advantageous vegetation types comprised 55.64 per cent of the study area. In the fall period, 39 (79.59 per cent) of the 49 home ranges included more than the expected amount of the advantageous types, while only 10 (20.41 per cent) included less than the expected amount. This would seem to indicate some selection of the advantageous types and avoidance of the disadvantageous types. In the spring period, there was no clear-cut evidence of any selective behavior. Only 24 (61.54 per cent) of 39 home ranges included more than the expected amount of favorable vegetation types, and 15 (38.46 per cent) included less than the expected amount. The inclusion of unfavorable as well as favorable vegetation types within the home range of most of the beach mice is apparently the result of the mosaic distribution of the different types. In the fall the average number of vegetation types per home range was 4.1, and in the spring it was 4.4. The home range of 1 mouse included areas of all 8 vegetation types. No home range was limited to a single type, but 6 of the 88 ranges included only 2 types.

Activity Within the Home Range

The home range of a mouse is the area to which the activities of the animal are chiefly limited. Food gathering and feeding, mating and play, and the maintenance of several homes and subsidiary holes appeared to be responsible for most of the nightly movements of established, resident beach mice. The evidence comes mostly from track records. The tracks leading from a particular hole usually included one or more beaten trails to places where foods were abundant. The food plants most frequently visited were the bluestem (*Andropogon maritimus*) and sea oats (*Uniola laxa*). The fruits of the bluestem were readily available to the mice, but those of the sea oats usually attainable only after they had been blown down by heavy winds. Places where sea-oats fruits were blown down and drifted into windrows were frequently the terminus of much traveled mouse trails. Some beaten trails in the Beach Dune, Sea Oats Interior Dune, or Bluestem Interior Dune habitats terminated in dense stands of bluestem. The beaten trails, the result of numerous round trips to the same place in a single night, are attributed to food-storage activity, for foods from the spot visited were found stored in burrows which were excavated. Some excursions apparently involved feeding rather than the gathering of food for storage. Single trails, quite different from the beaten paths described above, often represented activity in the vicinity of food plants. A trail of this sort would lead in a more or less direct line to the food plant, meander about considerably in the vicinity of the food, and then lead on but away from the hole. Although it is difficult to distinguish the types of activity involved from tracks left in the sand, evidently feeding or food gathering accounted for or was connected with most of the nightly trips of a beach mouse.

Movements associated with reproductive activity can scarcely be identified from the track records. Beach mice tend to pair rather permanently, with the male and female sharing the same hole or a number of holes within their more or less common home range. Movements in search of a mate, therefore, would be the exception rather than the rule in the case of permanently established, resident animals. Some mouse trails were suggestive of play activity or, possibly, of activity associated with sexual behavior. In some areas there were tracks that indicated that one or more mice had done a great deal of running in circles. In other areas the trail of a single mouse indicated movement of the animal in circles or in the form of a figure eight. Since all trails of this type were in areas barren of cover or food, it is very unlikely that they had anything to do with feeding or food gathering.

The mouse trails frequently led from one to another of the several holes used within the home range. After a blow had drifted the holes shut with sand, several or all of the normally utilized holes in the home range would be visited and cleaned out in the course of a night's wandering. This suggests, at least, some conscious maintenance of the various holes by the mouse. That the mice knew the location of the holes within their respective areas of activity was shown on many occasions when mice were released from traps. Often a mouse would go to a hole that had been completely obliterated by drifting sand, open the hole, and go in. Once a young adult male, resident on the plot for the previous 11 days, became chilled in the trap and was kept in captivity overnight. When released next day at the point of capture the mouse went 18 feet and opened up a hole that had been completely obliterated by wind and rain and entered it. Some trails led into and again out of holes occupied by the ghost crab. Whether the mice entered these crab holes in search of food, out of curiosity, or to escape a possible predator cannot be known with certainty.

The amount of activity of a mouse on a given night surely is influenced by several factors. Hunger, urge to store food, sex drives, need for exercise, and possibly other factors must affect the amount of nightly travel within the home range, but it seems impossible to evaluate fully the effects of these factors. The most potent factor affecting amount of activity appears to be the amount of illumination of the environment. The beach mice were very active on dark nights, and they showed little activity on clear nights during the full of the moon. It has been shown (Blair, 1943*a*) that differences in illumination equivalent to the differences between a clear moonless night and a clear half-moon affect the activity of some species of small mammals. In the present field observations it was difficult to differentiate between the effects of illumination and the effects of such physical factors as temperature, humidity, wind velocity, and rainfall. In general, the mice were most active on stormy, rainy nights. This weather may have had some effect on activity, but it is also significant that these were also the darkest nights. After clear, moonlit nights many of the mouse holes had no trails leading from them or only a few short trails. In one instance it was established that a mouse did not leave its hole on a clear night two days past the full moon. This was a female which was not caught in a hole trap until the second night it was set. The first night, which was clear and cloudless, the mouse did not leave its hole, but the second night, which was cloudy and overcast, the mouse was in the trap.

The effects of illumination and of other factors of the physical environment on the amount of activity are illustrated by a comparison of captures in the traps under different conditions of the moon and the weather. On the clear night of November 29, 1941, 4 days before the full moon, 17 beach mice were caught on a segment of the plot. On the following night, which was partly cloudy with the moon obscured most of the night, the same traps took 28 mice. On the clear night of December 5, 1941, 2 days past the full moon, 13 mice were caught on a segment of the plot. On the following night, which was cloudy and overcast, the same traps took 28 mice. On the clear night of December 11, 1941, with the moon entering the third quarter (approximately half-moon, rising about midnight) 20 traps in the beach dunes took only 4 mice. On the following night, with drizzling or pouring rain all night, 19 of these traps took 14 mice. On the night of January 3, 1942, 1 day past the full moon, with the temperature well above freezing and with rain and wind most or all of the night, 41 mice were caught on a segment of the plot. On the following night, with a light overcast and with a temperature of about 33°F., only 25 mice were caught on the same area. On the next night, with clouds in the evening, clear in the morning and with the temperature about 28°F., only 22 mice were caught on the same area. Other records could be cited, but these seem sufficient to indicate that the catch was much smaller when there was the illumination of from a half to a full moon than when the moon was obscured by clouds.

That illumination is of greater importance than meterological conditions in influencing the activity of the beach mice is seen from records of capture during the dark of the moon. On May 20, 1942, 4 days after the new moon, it was partly cloudy in the evening and cloudy in the morning, and 43 mice were caught on a segment of the plot. On the next night, with similar cloudiness and a shower before dawn, 36 mice were caught on the same area. On the following night, which was clear and cool, 44 mice were taken on the same area. On another segment of the plot, 21 mice were taken on the clear night of May 18. On this same segment, 24 mice were taken the following night, which was cloudy with a shower in the night. The conclusion is that, with the factor of illumination by the moon removed, the mice seemed to be no more active on cloudy than on cloudless nights.

The distances that a mouse travels in a night are revealed by the trails left in the sand. Records of 65 sets of trails emanating from a mouse hole were made. Each trail was followed until it returned to the hole or until it was lost in other trails, in dense vegetation, or on hard ground. The trails indicated that on any given night the activity of a mouse centered about one or more holes within its home range. The mouse did not leave the nest, wander during the night, then return to the nest before morning. Instead, there was evidence that it made numerous round trips away from and back to the hole. The trails usually radiated out from the hole like the spokes of a wheel, but were seldom of the same length. All of the meanderings of a trail were not plotted, but a record was made of the direction and greatest distance reached from the hole. The number of trails leading from a hole varied from 1 to 9 and averaged 4.3. This gives the number of directions the mouse traveled from its hole, but not the number of trips, as a trail to a food plant might show as many as 10 or more round trips in the course of a night. The length of the trails varied greatly, as would be expected. In the 65 sets of tracks, the shortest trail reached an average distance of 85.4 feet from the hole. The minimum was 15 feet and the maximum for the shortest trail in each set was 240 feet. The longest trail in a set reached an average distance of 261.8 feet from the hole. The minimum was 105 feet, and the maximum was 789 feet. All 65 sets of tracks were believed to have been made by resident, sexually mature mice. It is not likely that all tracks in a set were always made by a single mouse, for a male and female frequently occupied the same hole, nor is it certain that the tracks from a single hole represented all of the nightly activity of a mouse or pair of mice. Many of the mice utilized more than one hole, and sometimes tracks radiated out from several of these holes after a night's activity. These data indicate, however, that the focus of activity is the hole (or holes) and they give the maximum distances that a resident mouse may travel from its home in a single night. The amount of movement in the home range by a pair of beach mice in a single night is shown in Figure 2C.

The movements of the mice were influenced to some extent by the location of the traps. Traps were left open and unset at times on some segments of the plot. At such times beaten trails indicated that the mice were visiting certain of the traps and storing the sunflower seed used as bait, and some of these food stores were observed in holes that were excavated. Some of the mice learned to follow the trap lines. In one case a trail presumably made by a resident female indicated that this mouse moved 110 feet to a trap in the nearest line and then followed this line for a distance of 560 feet, visiting each unset trap. Some effect of the traps on the mice is no more than might be expected upon introduction into the area of a considerable supply of a food delicacy. There was no indication that the mice abandoned their use of native foods. They simply supplemented them with the sunflower seeds.

Permanence of the Home Range

All of the evidence indicates that once a beach mouse settles in an area it usually remains there for the duration of its life. Twenty-one beach mice that were living on or near the plot when trapping was discontinued in mid-January were still alive there when field work was resumed in early May. Three of these were juveniles in January, and all had moved considerable distances in the interval between the two periods. The 18 other mice were established residents in January. Sixteen of these showed no shift in the location of the home range, although the area was not exactly the same size in the 2 periods. Two others showed a slight shift in the location of the home range, but even in these cases the spring range overlapped the fall range.

One slight shift in the ranges of a paired male and female was observed in December, 1941. The principal home of this pair was in an area of vegetated flood basin and under a large raft that had drifted onto the island during some past storm. A storm on December 23 filled the flood basins of the island with rain water and with water driven onto the island from the Gulf by a strong onshore wind. After this storm, which caused the flooding of a considerable part of their home range and of their principal home, the 2 mice moved to a nearby area of scrub dune which they had previously avoided. They continued using this new area at least until the work was discontinued on January 13, even though the water had subsided from their old area.

Even though the home range of a mouse usually remained in the same area, the actual holes utilized might change from time to time. The records of 7 individuals that were on the plot in both fall and spring and that had fairly adequate hole records are interesting. Only 2 of these 7 mice were still using, in the spring, one or more of the holes they had used in the fall. One was using 1 old hole and the other was still using 2 of its old holes. In other words, only 3 of the 36 holes used by these 7 mice in the fall were still being used by the same mouse in the spring. Six of the 36 holes had been taken over in the spring by different mice from those which had used them in the fall. Twenty-seven (75.0 per cent) of the holes used by these mice in the fall had apparently been abandoned by spring. These 7 mice were known to be using a total of 51 holes in the spring. These included the 3 that had been used previously by the same mouse and 20 that had been used in the fall by some other beach mouse. Twenty-eight (55.0 per cent) of the 51 holes were presumably new ones (that is, there was no record of their having been in existence in the fall). It appears from these data that the availability and location of a particular nest site has little to do with the location and permanence of a beach-mouse home range. The resident mice remain in a particular home range presumably because of sociological factors and available supply of food and cover. Holes are easily dug in the sand by the mice, and many holes of the ghost crab are available for utilization. The holes are frequently obliterated by drifting sand and, while there appears to be a considerable effort to maintain the holes in the home range, it seems likely that some holes are simply abandoned after they have drifted over. Nest and refuge holes might be more permanent and might be of more importance in limiting population density and determining home-range location in areas where holes are less easily made. On Santa Rosa Island they seem to be of minor importance to the beach mice because of the ease with which they are made and because of the large supply of ghost-crab holes.

Reliability of Trap Estimates of Home-range Size

The reliability of estimates of home-range size made on the basis of live-trapping records has been questioned by two recent workers (Hayne, 1949, and Howard, 1949). Before bringing the present data to bear on this question it would be well to examine the commonly held concept of a home range. The concept that is held by most recent workers has been stated by Burt (1943) as, "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young." This is a loose definition principally because of the multitude of meanings that may be given to the word "normal." To distinguish between normal and abnormal in relation to an animal's movements may at times prove very difficult. The difficulty in defining home range precisely stems largely from the fact that one is attempting to state in static terms (that is, in terms of square feet or acres) the area of activity of a living mobile animal that may have its movements influenced by a great many factors in the physical and biological environment. Most information about the home ranges of small nocturnal mammals has come from records of repeated captures of marked individuals in live traps. Repeated captures of an individual establish points that limit the area of the estimated range of that animal. This estimate of home-range size is certainly a crude estimate of the actual area ranged over, but it is by far the best estimate that has yet been obtained for the home range of a small nocturnal mammal. Only in the rarest of circumstances will the estimated home-range area correspond exactly to the area of movement of the animal.

Both Hayne (1949) and Howard (1949) criticize the estimation of the home range by means of traps, on the grounds that captures in traps near the homesite will interfere with movements of the animals and reduce the chance of their capture in traps at greater distances from the home. Both workers apparently refer to a trapping plan under which all traps in a gridded plot are left set continuously for a considerable period of time. This was the method used in the early home-range studies (Blair, 1940; Burt, 1940). With continuously set traps, it is reasonable to assume that captures near the home would limit the activity of the animal and that the estimated home range would be smaller than the area over which the animal would have traveled if there had been no trapping. This problem of underestimation was recognized at an early date in home-range studies and certain changes in trapping techniques developed to minimize the error in home-range estimates due to this effect. Blair (1942) trapped alternating lines in a grid on alternating periods of 7 days each, and in addition left a trap unset overnight if a particular animal had been caught in it the 2 preceding nights. Blair (1943*b*) also divided trapping plots into different segments, which were trapped on alternating periods, and in addition left a trap unset overnight if a particular animal had been caught in it the 2 preceding nights. In this study an even more complex system of trapping alternate lines, alternate sets of lines, and alternate segments of the plot was used, as well as the practice of leaving a trap unset for a night after a mouse had been caught in it for 2 successive nights. All of these methods serve to minimize the localization of an animal's movements by a trap or group of traps near its homesite or homesites. Hayne's discussion of the probability of capture of an animal at varying distances from its home applies only to the relatively simple situation in which all traps in a grid are left set continuously. It would not apply to the data of the present study, in which computation of the probability of capture in any given trap under the conditions of trapping would be an exceedingly complex problem. Whether or not estimates of home-range size obtained by the methods used with the beach mice actually are indicative of the areas of activity of these mice may be answered in part by other observations on these mice. The tracks of the mice should give some idea of their range of movement, and the location of the holes to which the mice went upon release from the traps should offer some clue to the reliability of the trap-estimated home ranges.

The tracks of an individual mouse in the sand are the best unbiased measure of the home range of that mouse. Utilization of track records, however, presents certain inherent difficulties. The mice left conspicuous trails on the loose white sand covering most of the island, but it was difficult to relate the trails to specific mice. Only when a single individual was known to occupy a certain hole and when the population density was thin was it possible to attribute a set of tracks to a particular mouse. Even then there could be no absolute certainty of the identity of the mouse that made the trails. The track records do, however, give an indication of the area of activity of the mice and, consequently, do serve as a check on the reliability of the trap-estimated home range.

Seven males that had an average trap-estimated range of 5.98 acres, based on an average of 15.28 captures each, were tracked on from 1 to 3 different mornings. If the area covered by the tracks is added to the area computed from the trap records, the average range revealed by the combined data is 8.30 acres. This indicates that the animals tend to range more widely than is shown by the trap records alone. The data are few, however, and not very consistent. In 4 cases the tracks did not extend appreciably beyond the trap-estimated range. In another, an extreme case, the trap records plus track data included an area of 14.50 acres, while the trap-indicated range comprised only 3.78 acres.

Seven females that had an average trap-estimated range of 4.69 acres, based on an average of 15.64 captures each, were tracked on 1 to 2 different mornings. Inclusion of the track records increased the average known range of these mice to 5.97 acres. The data for the females are more consistent than for the males. In 6 cases the tracks of the females extended little or not at all beyond the trap-indicated range. In the seventh case, the trap-indicated range was 2.81 acres, and the range based on both trap records and tracking was 4.20 acres.

Track records of a pair of mice that were for a considerable period the only residents on one area of the island tend to indicate that the trap-estimated home range is a fairly reliable estimate of the region over which an animal actually wanders. The tracks of these mice were recorded on 10 different mornings (Fig. 2B). It is impossible, of course, to distinguish between the tracks of the male and of the female. The area of activity of the pair, as indicated by the track records, showed a striking similarity to the smaller home range, that of the male, as indicated by trap records. Only one trail led outside the limits of the estimated home range of the female.

The location of the holes to which the mice went after release from the traps also serves as a check on the reliability of the home range as estimated from trap records. The mice for which home ranges have been calculated from trap records were followed to holes a total of 856 times. They went 822 times to holes within the estimated home range and only 35 times to holes outside the estimated range. Thus 96.0 per cent of the time they went to holes within the estimated range, but only 4.0 per cent of the time to holes outside of it. The holes used outside the estimated range were, on the average, 112 feet distant from the nearest border of the calculated range.

For purposes of comparison with the trap-estimated home range the track data may be treated in another way. Purely for purposes of discussion, and with strong reservations as to the validity of the assumption, it may be assumed that the longest trail of a beach mouse from its hole represents the radius of a circular area of activity of that mouse. It is not suggested that the home range of a beach mouse tends to be circular, nor that this estimated area is truly representative of the area of activity of the mouse. Trails of different lengths led in different directions from the mouse holes. This area, estimated with the longest trail as the radius of a circle, represents, therefore, a hypothetical maximum estimate of the area of activity as determined from the track records.

The average distance from the mouse hole reached by the longest trail in each of the 65 sets of tracks discussed earlier was 261.8 feet. Using this as the radius of a hypothetical circular area of activity about the hole, the calculated area of activity or estimated home range was about 4.95 acres. These track records were made in the fall of 1941 in areas other than the beach dunes. The average trap-estimated home range in these areas in the fall comprised 6.38±.81 acres. The hypothetical area of activity as estimated from the track records proved, therefore, to be somewhat smaller than the trap-estimated home range. But the 2 estimates are close enough to lend support to one another. There seems no reason to believe that the estimate of the home range made from trap records was too low because movements of the mice had been localized by a particular trap or set of traps.

Hayne (1949) has suggested the use of a point, established by taking the 2-dimensional average of the points of capture, which he proposes to call the "center of activity." When this method is applied to the beach-mouse data, the point usually falls near the middle of the home range as estimated by conventional methods. This measurement seems, therefore, to be directly related to the trap-estimated home range. It may be of some value when used in conjunction with the trap-estimated range, but when used alone, it sacrifices a majority of the information conveyed by the trap-estimated home-range data. Hayne, in his discussion of probability of capture at varying distances from the apparent center of activity, assumes equal probability of capture at equal distances. Statistically, this is a sound assumption; biologically, it is not. Movements of the beach mice were not at random for both the trap and track records showed that they definitely avoided certain areas. The records for a paired male and female mouse illustrate this point (Fig 2A). A major part of the activity of this pair centered about a hole near one edge of their respective ranges, although other holes were used to some extent. Not until much of their range was flooded during a storm, were these mice ever caught in a nearby scrub-dune area, nor did their trails lead there. It was evident that the mice avoided this area.

Hayne's use of the term "center of activity" for the average point of capture seems particularly unfortunate in view of the behavior of the beach mice. The phrase "average point of capture" would probably be a better term for this statistic. Hayne seems tempted to associate the average point of capture with a true center of activity, which is the area in which the activities of the animal are concentrated. The track records of the beach mice prove that activity in the home range may shift from one to another of several different holes within the range. The true center of activity would shift correspondingly, therefore, from time to time; whereas the "center of activity," as defined by Hayne, would be fixed by the points of capture in the traps.

SOCIAL BEHAVIOR

A considerable amount of information was obtained concerning the relationships between individual mice and other mice of the same or different sex, age, and residence classes. Most of this information came from multiple captures in traps (two mice caught simultaneously in the same single-catch trap); from captures at the same place on the same night but in different traps; and from the behavior of the mice in going to holes after release from the traps.

Association of Individuals

An adult male and adult female were caught simultaneously in a single-catch trap on 10 different occasions. This involved 9 different females and 9 different males, as one male and female were taken together twice. This indicates association of males and females during feeding activities, as the mice had to enter the traps together in order for both to be caught in the single-catch traps. On 4 occasions, 2 adult males were taken in a single-catch trap, which suggests a certain amount of tolerance of 1 male for another. On no occasion were 2 adult females taken in the same trap, which suggests less tolerance between adult females than between adult males. An adult female was once taken in the same trap with an immature female, and another adult female once in the same trap with an immature male. On 5 different occasions an adult male was taken in a trap with an immature female. On 1 occasion 2 immature females were taken in the same trap.

Capture of 2 individuals at the same place on the same night but in different traps gives a less positive measure of the association of 2 individuals than does a capture of the two in the same trap, since it indicates only that the 2 visited the same spot on the same night. They may have visited the spot at different times and may have been caught at different times of the night. They may have been traveling together but may have entered different traps. Two adult mice were caught in different traps at the same spot and on the same night a total of 214 times. Observed and expected frequencies of the different combinations of sexes are shown in Table VII. Expected frequencies are based on the ratio between resident males and females during the entire period of the study. The combination of an adult male and female at a spot occurred significantly more frequently than could be expected on the basis of chance. The combination

TABLE VII

COMBINATIONS OF ADULT MICE CAUGHT AT SAME SPOT ON SAME NIGHT BUT IN DIFFERENT TRAPS

Expected frequencies are based on sex ratio on plot.

Combinations	Frequencies		$(X-m)^2/m$ Chi-square
	Expected (m)	Observed (X)	
Male plus male	68.0	47	6.485
Female plus female	39.1	29	2.609
Female plus male	106.9	138	9.046
Totals	214	214	18.140

of 2 females occurred in a frequency that did not differ from what might be expected on the basis of chance. The observed frequency of the male plus male combination was less than the expected. This deviation is significant, for its chi-square value approaches the 1 per cent level of probability. The records indicate at least that the combination of an adult male and female at a particular spot on a given night occurred more frequently than the combination of female and female or male and male. In this they add weight to the evidence from the multiple captures that paired males and females tended to be associated in their nightly travels on the plot.

Behavior of the mice after they were released from the traps provided some very interesting information about the social behavior of these animals. On 2 occasions, 3 mice went to the same hole on the same morning. In one case 3 adult males went to the same hole, and all stayed down the hole. This, on the basis of other observations, indicated that no fighting took place. In another case an adult female and 2 adult males went to the same hole and gave no indication of any antagonism. Four times an adult female and an immature female went to the same hole, and 3 of these times the immature female was chased out by the adult.

On 65 occasions 2 adult beach mice went to the same hole on the same morning (Table VIII). The frequency with which 2 males went to the same hole is slightly less, though not significantly less, than would be expected on the basis of chance. The frequency with which 2 adult females went to the same hole is considerably less than would be expected by chance alone. The deviation is significant, for its chi-square value lies between the 1 per cent and 5 per cent levels of probability. An adult male and female went to the same hole a total of 48 times, which is significantly in excess of the expected frequency for this combination. In 3 of the 13 times when 2 males went to the same hole 1 male was chased out by the other. In 3 of the 4 times when 2 females went to the same hole one was chased out by the other. In 3 of the 48 times, when a male and female went to the same hole, the male was evicted by the female, but

TABLE VIII

USE OF SAME HOLE AFTER RELEASE FROM TRAP BY DIFFERENT COMBINATIONS OF ADULT MALES AND FEMALES

Frequencies of event of two mice going to same hole on same morning after release. Expected frequencies are based on sex ratio on the plot.

Combinations	Frequencies		$(X\text{-}m)^2/m$ Chi-square
	Expected (m)	Observed (X)	
Male plus male	20.6	13	2.804
Female plus female	11.9	4	5.252
Female plus male	32.5	48	7.392
Totals	65	65	15.448

once the male chased out the female. The data on hole sharing indicate that the males and females were associated in use of the den holes. They indicate strong antagonism between adult females and considerably less antagonism between adult males.

Sex Pairing

Examination of data for the association of individuals indicated that sexually mature male and female beach mice pair and remain paired over a long period of time, presumably for as long as both of the partners live. Similar behavior has recently been reported for a related species, *Peromyscus maniculatus,* by Howard (1949), who used nest boxes to obtain his data. The data for the beach mice was chiefly from multiple captures in single-catch traps. Capture of two individuals at the same spot on the same night but in different traps was not considered by itself sufficient evidence of pairing, but was helpful in identifying the pairs.

In the fall period, 23 (56.10 per cent) of the 41 resident, sexually mature females recorded on the plot were each paired with a sexually mature, resident male. The 2 mice of a pair were taken together in the same trap an average of 0.30 times. They were taken in different traps at the same time and place an average of 1.74 times. They went to the same hole on the same morning an average of 0.70 times. They went to the same hole but on different mornings an average of 2.26 times. The known home ranges of the 2 mice of a pair overlapped 77.35 per cent on the average. By overlap is meant the fraction of whichever range is smaller that falls within the larger home range. Each of the 23 females produced at least 1 litter during the fall period. Six produced 2 litters each, and 3 others possibly produced 2.

One male and female remained paired from the fall period at least to the end of the field work in June. The known period over which these 2 mice were paired was 179 days. Twelve of the 23 pairs remained unbroken to the end of the fall trapping on January 13. Only 2 of the 24 mice involved survived to the spring. A female whose fall mate did not survive to spring was paired in the spring with a male whose mate disappeared after the fall period. Five pairs were broken during the fall trapping by the death or disappearance of the male. In 4 cases the male died in a trap due to cold or drowning during a storm, and in 1 case the cause of disappearance is unknown. In 1 instance the surviving female formed a new alliance with an immigrant male that was first taken on the plot a week before the death of her old mate. There is no evidence that the 4 other surviving females remated after the disappearance of their mates. Two of these females had shown some association with second males before the death of their mates, and it is possible this association continued, although there is no evidence of it. Three pairs were broken by the disappearance of the female during the fall period, but the cause for the loss of the females is unknown. In 2 instances, both the male and the female of a pair disappeared during the fall period. In one of these last cases, the female survived the male by a month, but there is no evidence that she remated. A fairly monogamous society is indicated by the fact that only 2 of the 23 paired females showed any association with more than 1 male so long as that male remained alive on the plot.

Eighteen (43.90 per cent) of the 41 adult females that resided on the plot at some time during the fall period showed no positive evidence of pairing with a male. The records of 3 of these are incomplete and probably are not sufficient to show whether or not there was pairing. Three others showed possible evidence of pairing. Each was caught on 3 different occasions at the same spot with a particular male. The average overlap of the known ranges with the ranges of the presumed mate averaged 85.33 per cent. One of these females produced 1 litter. There is no evidence that either of the other 2 produced a litter, but both appeared to be sexually active. Twelve females had records that gave no clue to a possible mate. Nine of these produced 1 litter each, and 1 produced 2 litters. Two produced no litter. One of these 2 appeared to be sexually active; the other did not. It cannot be said from the data whether the apparently unpaired females were promiscuous in their sexual behavior for the evidence is insufficient to indicate the mates of all of the breeding females on the plot.

So far the pairing of the beach mice has been considered primarily with respect to the population of adult females. The 24 males that associated with the 23 females represent only 42.10 per cent of the total number of 57 mature males that resided on the plot at some time during the fall trapping. Three males, in addition to the 24, showed possible pairing with females on the basis of captures at the same time and place in different traps. Thirty males showed no evidence of association with any female. There were, therefore, twice as many unpaired males as females. Even if the 15 females for which there is no evidence of pairing actually did have mates among these apparently surplus males, there was still a surplus of 15 unpaired sexually mature males. It is impossible to be certain, of course, that some of the litters produced by even the paired females were not sired by some of these unpaired males. In 2 cases a female showed some association with a male other than the one with which she was usually associated. The implication is strong, however, that the male with which a female usually associated was probably the sire of her offspring. Two paired males showed some association with a second female. One male was taken at the same time and place with a female other than the one he usually associated with, and when released both went to the same hole. Another male was taken in the same trap with a female other than his usual associate.

Pairing in the spring period was about the same as in the fall except for certain minor differences. Twelve (50.00 per cent) of 24 females that resided on the plot at some time during the spring period showed positive evidence of pairing with a resident male. The apparent mates were taken simultaneously in the same trap an average of 0.08 times. They were taken in different traps at the same time and place an average of 1.42 times. They went to the same hole on the same morning an average of 1.17 times. They went to the same hole on different mornings an average of 2.17 times. The estimated home ranges of the paired mice showed a 79.75 per cent overlap. Ten of the paired females had 1 litter each during the spring period, and 2 had no litter, although both appeared to be sexually active. Nine of the 12 pairs remained unbroken to the end of the spring field work. One of these pairs, discussed earlier, had existed from the previous fall. One pair was broken by the disappearance of the male. The female of this pair had shown some association with a second male before the disappearance of her mate, but there is no record of her association after his disappearance. The paired females in the spring showed more tendency to associate with other males than did the paired females in the fall. Seven of the paired females gave no evidence of association with any male other than the presumed mate so long as he was alive. Three showed some association with a second male. One showed some association with 2 other males. One showed about equal evidence of association with 2 males. The apparently greater promiscuity of the females in the spring possibly resulted from the much greater excess of mature males than there was in the fall.

Four other females in the spring showed slight evidence of association with 1 or more males, but it is not possible to determine from this evidence whether or not they were paired with a particular male. One of these females went to a hole with a male on one occasion and to a hole with another male at another time. This female produced 1 litter. Another female was taken 3 times at the same time and place with a male whose home range overlapped hers 79 per cent. This female also bore 1 litter. In 2 instances a female was caught twice at the same time and place with one male and twice at the same time and place with another male. One of these females produced a litter. The other did not, although she appeared to be in breeding condition. Eight females showed no evidence of association with a male. Only 2 of these produced a litter each, while the other 6 bore no young, although all appeared to be sexually active.

The surplus of presumably unpaired males was proportionately greater in the spring than in the fall. Fifty-six mature males resided on the plot at some time during the spring period. Twenty-three (41.07 per cent) of these males showed some evidence of association with 1 or more females. One of these showed about equal evidence of association with 2 different females. One was taken once at the same time and place and went to the same hole with a female other than his usual mate. Thirty-three (58.93 per cent) of the 56 males gave no indication of pairing with any female. Mature, unpaired males, therefore, exceeded mature unpaired females in the ratio of about 4 to 1, as there were only 8 mature females that gave no evidence of association with males in the spring period. The apparent decrease in monogamous behavior in the spring possibly results from this excess of males over females. Even with some of the breeding females tending to associate with more than 1 male there was still a large fraction of the mature male population that showed no association with a female.

Some clues to the organization of the beach-mouse society are given by these observations. The mice showed a strong tendency toward monogamy during the breeding season, with a mated pair tending to remain associated so long as both remained alive. Some individuals of both sexes gave no evidence of pairing, although they appeared in some cases to be sexually active. There was an excess of unpaired males over unpaired females in both the fall and spring. In the spring, when the excess of males over females was greatest, the mice seemed to be less strongly monogamous than in the fall, when the excess of males was least. Adult females were intolerant of other adult females, but they were generally tolerant of individuals of other sex and age classes. Two adult females were never taken simultaneously in the same trap, and in 3 of the 4 times when 2 females went to the same hole 1 female drove the other out. Adult males were more tolerant of other adults of the same sex than were adult females. Two adult males were caught simultaneously in the same trap on 4 occasions. Two adult males went to the same hole on 13 occasions, and only 3 times did one male chase the other out of the hole. In the wild population the beach mice did not seem to approach the extremely sociable behavior that has been observed in laboratory populations (Blair and Howard, 1944). In the laboratory, 2 pairs of beach mice lived peaceably together, and the females raised their young in the same nest, even taking turns nursing them.

FACTORS AFFECTING SURVIVAL

Many factors affect the chances of survival of an individual in a wild population of animals. The survival to sexual maturity of sufficient individuals to produce a succeeding generation is, of course, essential to maintenance of the species population and to perpetuation of the species. Differential survival of different genetic types in the population is presumably the chief agent of organic evolution. The environment in its entirety acts to conserve advantageous mutations and genotypes and to discard disadvantageous types. It is easy to generalize about the factors of the physical and biological environment that might affect survival in a natural population. In the case of small nocturnal mammals, however, it is difficult to obtain exact information about the relationship between a given species and the problems of survival in the environment in which that species lives. Some information of this nature was obtained for the beach mice, because the biotic community in which these mice were studied was a rather simple one containing only a few species of vertebrates. Observation of the mice was comparatively easy, after they were released from the traps, because of the sparse and open nature of the vegetational cover on much of the island.

Factors of the physical environment were of relatively little importance to the survival of the beach mice. The mice were active during tropical storms involving moderate wind velocities and heavy rainfall, and more mice were generally caught on rainy nights than on clear ones. The mice were active on nights when the temperature dropped below freezing. A few mice died in the confines of the traps on such nights, but there is no indication that either cold weather or storms normally had any fatal effect on the mice. Some of the mice were forced to change their home ranges when low parts of the island were flooded by rain and sea water during a tropical storm. At such times the mice may have been more vulnerable to predators, as they were moving from familiar to less familiar or strange terrain, but there is no evidence of such vulnerability. Wind-blown sand often obliterated the holes of the mice, but the mice reopened the holes after the blow, and there is no evidence that the closing of the holes had any direct effect on survival, although there might have been some indirect effect. If a mouse was chased by a predator before he had opened the holes within his home range, his chances of escaping the predator would be lessened. The mouse would have to return to the hole from which he had emerged or attempt some other means of escape.

Tropical hurricanes are probably the most important factor of the physical environment affecting the survival of the beach mouse. Much of the area of the low sand island is inundated during a hurricane. At such times the mice must either drown or become concentrated on the few high points such as the scattered scrub dunes on Santa Rosa Sound side of the island.

Diseases and parasites were rare and no critical effect on survival was noted during the time of the study. One mouse lost its tail through disease, but survived longer than did the average mouse. This mouse, a female, was first observed on December 11, 1941, as an immature individual, probably about four weeks old. At that time the tail appeared normal. Six days later the tail was greatly swollen. The next day the tail was hard and scabby. Four days later about one-half of the tail had rotted away. Five days later the tail was three-fourths gone. The stub of the tail was still sore 6 days later. This mouse survived until spring. There were no ectoparasites on the beach mice, and no check was made for internal parasites.

Occurrence of epilepsy in the wild population was one of the interesting discoveries of the field work. One adult male died in an epileptic seizure as it was being handled after removal from the trap. Another adult male had mild seizures while being handled on 4 different occasions. Another male recovered from a severe seizure on 1 occasion and had a mild seizure while it was being handled at a later date. One female had a mild seizure. Epilepsy is a recessive character in those strains of *Peromyscus* in which it has appeared (Watson, 1939). If that is true in *leucocephalus* the frequency of the recessive gene must be surprisingly high in the Santa Rosa Island population to account for the finding of 4 homozygous individuals among 329 mice handled. Assuming that epilepsy is recessive in *leucocephalus* and that all homozygous recessives among the 329 mice handled reacted, the recessive gene would have an estimated frequency of 11.02 per cent in the wild population.

The food supply seemed adequate at both seasons, but was more abundant in the fall than in the spring. The mice fed principally on the fruits of the bluestem (*Andropogon maritimus*) and sea oats (*Uniola laxa*). The fruits of several herbs were also eaten. The mice appeared to be well fed at both seasons. The greater concentration of mice in the beach dunes than in the other vegetation types might have been a response to the larger food supply there, but it could also have been a response to the better cover available.

Interspecific competition was certainly at a minimum and of little or no importance to the survival of the beach mice. The only other species of rodent was the cotton rat (*Sigmodon hispidus*), and that was apparently limited to a different vegetation type from those preferred by the beach mice. Beach mice did range occasionally into the edge of sedge marsh occupied by the cotton rats, but the cotton rats were never seen ranging out into the areas of open vegetational cover occupied by the beach mice. There was passive competition for food between the beach mouse and the ghost crab, because both fed extensively on the fruits of the sea oats. Yet the ghost crab provides holes for the beach mice. Many old crab holes were used regularly by the mice. Ghost crab holes are characteristic and easily recognized. They have 2 openings: one is in the form of a vertical "chimney"; the other enters at an angle and joins the chimney. Occupied holes of the crabs were frequently entered by the mice for trails of beach mice were frequently seen entering holes that had crab trails radiating out from them. Fruits of the sea oats were often stored in these holes, evidently by the crabs, and it is possible that the mice entered the crab holes to steal the food. The mice often entered the fresh crab holes after release from the traps, for temporary refuge. There was a suggstion that at times a mouse and crab occupied the same crab hole. One hole from which a crab was dug had 28 mouse trails radiating out from it, although there was then no mouse in the hole. Another hole had several mouse and crab trails radiating out from it, and a resident male beach mouse went to the hole when released from a trap. This male again went to the same hole the next morning. Two mornings later there were again fresh mouse and crab tracks radiating from the hole. These were the only instances noted of joint occupancy of a hole by a beach mouse and a crab, and the phenomenon appeared to be a rare one. The crabs probably benefited the mice most by making holes that were later used by the mice. They probably competed most with the mice for the fruits of the sea oats, an important food of both species.

Intraspecific competition may have had some effect on a mouse's chance for survival. The times in the life history of a mouse which would be most critical would be at the time of dispersal from the nest and the time of attempted establishment in a new area. A few young mice had wounds that indicated they had been in fights. In several instances resident mice, both male and female, chased out transient or immigrant young mice that invaded their holes. Establishment of a nest hole or holes is a critical event in the life of a maturing young mouse in a new area. That such young mice that attempted to use holes maintained by resident mice were driven out was evident. The greater concentration of beach mice in the beach dunes than in more open areas might possibly relate to intraspecific competition for food, but it might be concerned with a preference for the area of better protective cover.

Predation is probably the most important single factor affecting the chances of survival of a beach mouse, although few records of actual predation were obtained. Little is known about the specific predators on this species, but forms that normally prey on small rodents were present in the region. Shrikes (*Lanius ludovicianus*) learned to take the mice after they were released in the daytime, but being diurnal birds would not be normal predators on the nocturnal beach mice. Skunks (*Mephitis mephitis*) were known to have preyed on the mice. Sight records and trails indicated that at least 2, and possibly 3, skunks were ranging over the plot. One of these skunks appeared to be a mutant individual, in which the normally white stripes were a bright, lemon yellow. Beach mouse bones and hair were observed in the fecal pellets of the skunks, but they fed principally on crabs and beetles. Numerous snake trails were seen in the mornings, mostly in the vicinity of the beach dunes, evidence that nocturnal species of snakes were active on the island. No snakes were caught, and none was identified. Six species of owls occur commonly in western Florida (Bailey, 1925). Owls were heard calling on the mainland, but none was located on the island, possibly because little field work was done there at night.

The physical environment and the general ecological aspect of Santa Rosa Island must be considered in relating the behavior of the mice to the possibility of capture by a potential predator. The island was ecologically unfavorable for small rodents in many ways. The vegetational cover is sparse over extensive areas of the island. Only on the dunes fronting the Gulf beach and on certain scrub-covered dunes near Santa Rosa Sound is vegetation really heavy. White sand, nearly as white as snow, comprises the background on which these mice live and attempt to avoid potential predators. The high reflectance of light by this white sand makes even small objects stand out boldly on moonlit nights. The beach mouse and the cotton rat are the only representatives of what Elton (1935) calls "key industry species" on the island. In other words, the beach mice and the cotton rats, the latter limited in numbers by the small areas of suitable environment, must support the predatory species that choose to range on the island. The dearth of other rodent species presumably benefits the beach mice by eliminating interspecific competition for food and homes, but it also throws onto the beach-mouse population most of the burden of supporting any local predators that feed on small rodents.

Adaptations of the beach mice to escape capture may be either morphologic or behavioristic. On the morphologic side, the beach mice of Santa Rosa Island exhibit a coat-color pattern that is unique among *Peromyscus*. Mice of this genus usually have white underparts and dark-pigmented sides and dorsum. This is the typical pattern of countershading that occurs in most higher forms of animal life. Mice of the subspecies *leucocephalus* have the white of the underparts extending up onto the dorsal surface. Dark pigmentation is limited to the area of the mid-dorsal line. The general effect is that of a nearly white mouse with an indistinctly defined gray band along the mid-dorsal line. No complete genetic analysis of the coat pattern of these mice has been made. It is known, however, that this pattern results from the interaction of a major dominant gene and numerous minor genes that act to restrict the pigmented area (Blair, 1944). The *leucocephalus* color pattern has presumably resulted from the selective advantage conferred by the mutations toward restriction of the pigmented area. The least pigmented individuals, being less conspicuous on the white sand, have escaped from potential predators more readily than did the darker individuals. The rigor of selection against dark-colored individuals probably accounts, in part at least, for the fact that no individual even heterozygous for the recessive allele of the major pattern gene has been found in extensive mating tests of Santa Rosa Island mice against other *Peromyscus* that were homozygous for the recessive gene.

The Santa Rosa Island mice, living on a background with a high reflectance of light, have practically dispensed with countershading as a protective adaptation. Persistence of the indistinct, gray, mid-dorsal pigmentation seems likely to be due to the protective advantage of this pattern rather than to the fact that evolution has not yet succeeded in eliminating all dark pigment. The white sand of the island contains scattered fragments of pink, gray, brown, black, and yellow shells. So long as it doesn't move, a beach mouse blends into this background so readily that it is difficult to see even in broad daylight. A completely white mouse would probably appear more conspicuous than one with an indistinct, gray mid-dorsal area.

On the behavioristic side, the activities of the beach mice appeared to be chiefly controlled by the danger of capture by a predator. The mice were less active on clear, moonlit nights than they were on cloudy nights or during the dark of the moon, behavior which must seemingly be interpreted as a response to the greater possibility of detection and capture by a predator in bright moonlight. In nightly wanderings beach mice avoided barren areas lacking in vegetative cover.

The behavior of a beach mouse that was attempting to escape from a predator may be inferred from the behavior of the mice that were released from the traps. The situations are not strictly comparable, for a mouse might behave differently in daylight than at night, but it seems likely that the escape devices used in daytime were mostly instinctive ones that would be used under any circumstances. Resident mice usually ran directly to one of the several holes that each mouse maintained for nesting, food storage, or possibly refuge. The resident mice were well oriented and knew the way to their holes. A mouse released at the same place on different mornings usually took the same route to its hole. This was not necessarily the most direct route, for the mice traveled under the protecting cover of vegetation if possible and avoided open areas. If a mouse went to a hole and found it obliterated by drifted sand, the mouse would either dig its way in or go on to another hole. After entering a hole the mice would frequently plug the hole with sand from the inside. Mouse holes that were excavated and that had been made by the mice themselves, as opposed to the old crab holes frequently used, had a typical form. The entrance hole was usually located on the side of a dune and near the base of some plant such as a clump of sea oats. The tunnel led back to a nest chamber, and a second tunnel extended to a breakaway hole near the top or opposite side of the dune. This breakaway hole has been previously described for this species by Hayne (1936). Both resident and nonresident mice sometimes went to active crab holes near the point of release. The resident mice seemed to know the location of the crab holes within their home ranges, and very likely used them habitually as temporary refuges.

Transient and immigrant mice showed a greater variety of escape mannerisms than did residents for they seldom knew the way directly to a hole. These mice were presumably more vulnerable to predators than were the established residents, for they did not know the terrain as well. They seldom went directly to a hole in a way that indicated they knew exactly where they were going. Some of these mice hid in the bases of clumps of *Panicum amaralum* or *Uniola laxa*. Sometimes these mice hid in shallow holes not much larger than the body of the mouse. In such holes they were very difficult to see unless they moved. Many of these shallow holes were seen on the island. Fresh claw marks and tracks indicated that at least some of these holes were dug by the mice. In some instances the mice were seen to dig these shallow holes after release from the trap. In other instances the mice would cover themselves partially with sand in these shallow holes, and in them they were very difficult to see. When driven into open areas without vegetational cover the mice would sometimes stop, crouch low to the ground and remain motionless. A shrike that had been following me once struck a mouse that was exhibiting this "freezing" maneuver. The shrike watched the mouse stop then landed on the ground about 8 feet away. The bird pranced about for a few moments and then struck the mouse. Mice that did not go directly to a hole when released usually changed course by cutting back whenever they came to an area of vegetational cover.

SUMMARY

Population structure, social behavior, and environmental relations were studied in a beach mouse (*Peromyscus polionotus leucocephalus*) population on Santa Rosa Island, Florida, from November 5, 1941, to January 13, 1942, and from May 7 to June 17, 1942. Field methods included: (1) the live-trapping and marking of 328 beach mice on a 65-acre segment of the island and on adjacent areas; (2) the tracking of individual mice in the loose sand of the island to obtain a measure of normal activity; (3) the locating of holes used by

the mice by following the mice after their release from the traps; and (4) the recording of various observations on social behavior, foods, and predators.

The population density of beach mice varied from a low of only 0.82 individuals per acre in early November, when only 69 mice were recorded, to a high of 1.40 mice per acre in late December, when 117 mice were recorded. The resident breeding population showed less fluctuation than did the total population, but it did increase gradually in the fall and remained rather stable during the spring period. The sex ratio in the resident breeding population showed no significant deviation from the expected 1:1 ratio in the fall, but in the spring males were significantly more numerous than females. Much breeding activity was evident in the fall, and immature mice comprised a large fraction of the total population. Little breeding occurred in the spring.

The number of beach mice per average home-range area provided an estimate of the concentration or crowding of the mice. Females showed an average of from 1.36 to 2.56 individuals per home-range area. Males were more crowded than females, for they showed an average of from 1.92 to 4.24 individuals per average home-range area.

Changes in the population (Table IX) resulted principally from the immigration and settlement of young mice and from the disappearance of resident adults. An indication of the distance that a young mouse may disperse is given by 14 juveniles that moved an average, known distance of 1415±89 feet before establishing residence. The period of establishing residence in a new area appears to be a critical period in the life history of a beach mouse. The disappearance of resident adults presumably results principally from predation. Only 19.5 per cent of the mice resident on the plot in early January survived the 4-month period until early May.

The home ranges of males and females as estimated from trap records did not differ significantly in size. The home ranges of beach mice living in the comparatively dense cover of the beach dunes averaged significantly smaller than the ranges of mice living in the more open cover of other vegetation types. The home ranges of the mice averaged significantly larger in the spring than in the fall. Each estimated home range contained an average of about 20 mouse holes, of which an average of about 5 were entered by that mouse after release from the traps.

Eight microhabitats, distinguished principally by differences in vegetation, occurred in the study area. The average number of vegetation types per home range was 4.1 in the fall and 4.4 in the spring. The mosaic distribution of the vegetation types probably accounts for the fact that apparently undesirable as well as desirable types were included in the home ranges.

Movements of a mouse within its home range were principally for feeding and food gathering. Other motivations included exercise, sexual activity or play, and the maintenance of the several holes utilized within the home range. The degree of illumination by the moon was the most important factor govern-

TABLE IX

Change in Resident Population of Beach Mice

Date	Females				Males			
	Disappeared During Period	Maturation of Immatures Already on Plot	Young Adult Appeared	Old Adult Appeared	Disappeared During Period	Maturation of Immatures Already on Plot	Young Adult Appeared	Old Adult Appeared
Nov. 5-18, 1941	2	Not Calculated	Not Calculated	Not Calculated	1	Not Calculated	Not Calculated	Not Calculated
Nov. 19-Dec. 2, 1941	1	4	7	1	6	....	5	6
Dec. 3-16, 1941	6	2	1	....	6	3	4	....
Dec. 17-30, 1941	8	6	8	1	10	....	10	....
Dec. 31, 1941-Jan. 13, 1942	Not Calculated	8	....	....	Not Calculated	3	....	....
May 7-20, 1942	2	Not Calculated	Not Calculated	Not Calculated	4	Not Calculated	Not Calculated	Not Calculated
May 21-June 3, 1942	2	3	1	....	13	2	1	1
June 4-17, 1942	Not Calculated	1	....	1	Not Calculated	....	....	1

ing the amount of activity on a given night. Half moonlight or more inhibited activity of the mice. The location of the traps had some influence on the direction of movement of mice within the home range.

The evidence indicates that once a beach mouse settles in an area it usually remains there for the duration of its life. The actual holes utilized in the home range may change from time to time, which suggests that the location of a particular nest site has little to do with the location and permanence of a home range.

The area of activity as indicated by track records and the location of holes to which the mice went after release from the traps both indicate that the home range estimated from trap records is a fairly reliable estimate of the actual area over which a beach mouse habitually wanders.

Greater antagonism was evident between adult females than between adult males. In many cases a male and female mouse were associated regularly in food gathering and in sharing holes; this demonstrates a fairly monogamous social pattern. A mated pair tended to remain associated as long as both remained alive. Some adult mice of both sexes showed no evidence of pairing. Apparently unpaired males exceeded unpaired females in both the fall and spring. The behavior of the mice was less strongly monogamous in the spring, when there was a marked excess of males, than in the fall, when the sex ratio was nearly even.

Survival of the beach mice in nature seems normally to be little affected by factors of the physical environment or by such biological factors as disease, parasites, food supply, or interspecific competition. Intraspecific competition may have some effect on survival, particularly at the time a maturing mouse attempts to establish residence in a new area.

Predation is probably the most important single factor affecting the chance of a beach mouse for survival. The environment in which the beach mice live is unfavorable in several respects. Other species of rodents that might provide food for potential predators are scarce. The high reflectance of light by the white sand of the island makes even small objects conspicuous on moonlit nights. Vegetational cover is sparse over much of the area of the island. Adaptations of the beach mice for survival in this environment include: (1) a nearly white pattern of pigmentation that makes them inconspicuous on the white sand and (2) certain behaviorisms that assist the mice in escaping potential predators.

LITERATURE CITED

Bailey, H. H.

1925 The birds of Florida. Williams and Wilkins: Baltimore. xxi + 146 pp., 76 pls., 1 fig., 1 map.

Blair, W. F.

1940 A study of prairie deer-mouse populations in southern Michigan. Amer. Midl. Nat., 24: 273-305, 4 figs.

1941*a* A simple and effective live trap for small mammals. Journ. Wildlife Management, 5: 191-93, 1 fig.

1941*b* The small mammal population of a hardwood forest in northern Michigan. Contrib. Lab. Vert. Genetics Univ. Mich., No. 17: 1-10.

1942 Size of home range and notes on the life history of the woodland deer-mouse and eastern chipmunk in northern Michigan. Journ. Mammalogy, 23: 27-36, 1 fig.

1943*a* Activities of the Chihuahua deer-mouse in relation to light intensity. Journ. Wildlife Management, 7: 92-97, 1 fig.

1943*b* Populations of the deer-mouse and associated small mammals in the mesquite association of southern New Mexico. Contrib. Lab. Vert. Biol. Univ. Mich., No. 21: 1-40, 2 figs.

1944 Inheritance of the white-cheek character in mice of the genus *Peromyscus*. *Ibid.*, No. 25: 1-7, 1 pl.

1946 An estimate of the total number of beach-mice of the subspecies *Peromyscus polionotus leucocephalus*, occupying Santa Rosa Island, Florida. Amer. Nat., 80: 665-68.

1948 Population density, life span, and mortality rates of small mammals in the blue-grass meadow and blue-grass field associations of southern Michigan. Amer. Midl. Nat., 40: 395-419, 2 figs.

Blair, W. F., and W. E. Howard

1944 Experimental evidence of sexual isolation between three forms of mice of the cenospecies *Peromyscus maniculatus*. Contrib. Lab. Vert. Biol. Univ. Mich., No. 26: 1-19.

Burt, W. H.

1940 Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool. Univ. Mich., No. 45: 1-58, 2 pls., 8 figs., 2 maps.

1943 Territoriality and home range concepts as applied to mammals. Journ. Mammalogy, 24: 346-52, 1 fig.

Elton, Charles

1935 Animal Ecology. Sidgwick and Jackson: London. xxx + 209 pp., 8 pls., 13 figs.

Haugen, A. O.

1942 Home range of cottontail rabbit. Ecology, 23: 354-67.

Hayne, D. W.

1936 Burrowing habits of Peromyscus polionotus. Journ. Mammalogy, 17: 420-21.

1949 Calculation of size of home range. *Ibid.*, 30: 1-18, 2 figs.

Howard, W. E.

1949 Dispersal, amount of inbreeding, and longevity in a local population of prairie deermice on the George Reserve, southern Michigan. Contrib. Lab. Vert. Biol. Univ. Mich., No. 43: 1-50, 2 pls., 24 figs.

RAND, A. L. and PER HOST
1942 Mammal notes from Highland County, Florida. Bull. Amer. Mus. Nat. Hist., 80: 1-21, 1 fig.

WATSON, MARGARET LIEBE
1939 The inheritance of epilepsy and waltzing in *Peromyscus*. Contrib. Lab. Vert. Genetics Univ. Mich., No. 11: 1-24.

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